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THE INTERNAL ANATOMY OF THE ORDER MECOPTERA

By Edith Potter, Ph.D.

(Read 1st June, 1938.)

With Fifty-Three Figures.

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Introduction.

Tillyard's work on the Panorpoid complex directed attention to the comparatively small order Mecoptera. His extensive work on the relationships of the members of this complex is confined to external characters and to only three of these—the wing coupling apparatus (1918), the trichiation (1918) and the venation of the wings (1919). It was thought that a study of the internal anatomy might throw some additional light on the classification of this group. An examination of the literature on the internal anatomy of the Mecoptera showed that what little had been written was contradictory. Most of the work was confined to the Panorpidae, with some allusions to the Bittacidae and Boreidae, and no mention was found of the remaining families. Considering the importance of the Mecoptera in the Panorpoid complex further information seemed desirable.

Only four species of the order occur in Britain; three species of *Panorpa* and one of *Boreus*. Specimens of some of the other families were obtained from abroad. Dr. Needham of Cornell University very kindly provided male and female *Merope tuber* Newm. collected by him in 1930 and Dr. Tonnoir of the Department of Scientific and Industrial Research, Canberra, sent specimens of *Harpobittacus tillyardi* Esben-Peters., *Chorista australia* Klug. and some Nannochoristidae. The last, however, had been collected 12 years previously and were not dissectable. All these insects were preserved in alcohol. Some specimens of *Bittacus pilicornis* Westwood were obtained from a dealer in America and identified for me by Mr. D. E. Kimmins of the British Museum (Natural History). Mr. A. Downes sent me specimens of *Apterobittacus apterus* McL. from San Jose, California, and *Brachypanorpa carolinensis* Banks from Mount Mitchell, North Carolina. The specimens of *Boreus hyemalis* L. were found with the help of Mr. Hugh Main. It was thus possible to examine species of two of the subfamilies of Panorpidae—Panorpinae and Choristinae—and of the families Meropidae, Boreidae and Bittacidae.

It is realised that the material available is insufficient for anything like a comprehensive survey of the internal anatomy of the order; but, because no one

country possesses members of all the families of the order, the difficulty of obtaining representative material applies to any worker. It is hoped that the present paper will form a basis for a, later, more complete survey of the order.

Panorpa was chosen as the typical genus, because it is easily obtainable and because it has been the subject of most of the earlier work. The terminal segments of the female abdomen have been included because there has been considerable misunderstanding of their homologies; the terminology of Snodgrass (1931, 1933 and 1935) has been used where the homologies of the parts are clear. The mouthparts have been ignored, because those of most of the families have been studied in some detail by Otanes (1922) and Steiner (1930); the male external genitalia are also excluded, because, although the interpretation of their homologies is in considerable confusion, their description would greatly have increased the length of the paper. The respiratory system was not studied as most of the material was too old.

I wish to express my sincere thanks to Dr. Needham, Dr. Tonnoir, Mr. Hugh Main and Mr. Anthony Downes for their kindness and for the material which they gave me and without which the work could not have been done; and my thanks are also due to Professor J. W. Munro, in whose department the work was carried out; to Dr. O. W. Richards for his help and encouragement and to Mr. D. E. Kimmins for identifying my material.

Panorpa.

The species dissected were *Panorpa communis* L. and *Panorpa germanica* L., these being the two common species in this country.

There seems to be some confusion among earlier workers about the number of segments in the abdomen of the genus *Panorpa*. Stitz (1908 and 1926) on *P. communis* L., Miyake (1912) on *P. nipponensis* Nav.* and Esben-Petersen (1921) state that there are ten segments in the abdomen. Miyake (1912) considered that the 10th segment consists of two parts, the membranous apical part bearing the two segmented cerci and the anus. Snodgrass (1931) has shown that in the female of *P. consuetudinis* † there are eleven distinct segments, and Issiki (1933) working on the PANORPIDAE of eastern Asia stated that there are eleven segments in both sexes. The eleven segments are quite distinct in the British species, *P. communis* L. and *P. germanica* L. (fig. 41). In the resting position the 11th segment of the male is invaginated into the slightly cuticularised 10th segment. The two segmented cerci of the female are borne on the 11th segment (fig. 41). The male bears a pair of single segmented cerci on the distal margin of the 10th segment.

The alimentary canal (figs. 4, 6).

Although there are several descriptions of the alimentary canal of the genus extant—Miyake (1913), Loew (1848), Dufour (1841) and Stitz (1908 and 1926)—there is none which gives a full and accurate account of this organ.

The pharynx runs from the mouth, through the proboscis, to the head and consists of a narrow, ventrally cuticularised trough with a membranous dorsal roof (fig. 6). This roof is supported by muscles which are attached to the frons and clypeus. The muscles control the opening and closing of the lumen of the

* According to Esben-Petersen (1921), this species was misidentified as *P. klugi* MacLachlan in these papers (1912 and 1913).

† Dr. Snodgrass in a letter (1938) states that there is some doubt as to the validity of this species.

pharynx. The dorsal membrane of the pharynx is continuous with the epipharynx. The pharyngeal trough articulates with the ventral region of the hoop-like sclerite which surrounds the pharynx immediately anterior to the brain (pl.) This sclerite is deeply notched on its dorsal surface and in this notch lies the frontal ganglion of the oesophageal sympathetic nervous system (fig. 11). The hoop projects dorsally and is continuous with the outer membranous cast of the pharynx. Posterior to the hoop, the pharynx narrows slightly as it passes between the brain and the suboesophageal ganglion and it expands behind them to form a muscular chamber supported by numerous lateral and dorsal muscles. The pharynx passes into the oesophagus which contracts and runs posteriorly into the thorax, where it dilates to form the proventriculus. This lies partly in the pro- and partly in the mesothorax.

The structure of the proventriculus has been discussed in detail by Dufour (1841), Loew (1848) and by Miyake (1913), and my observations confirm theirs. Its shape is that of an inverted truncated cone, and from the outside it appears to contain a smaller, dark brown cone. When the organ is slit longitudinally, it may be seen that the walls of the cone are thick and are composed of an outer layer of longitudinal muscles and an inner layer of circular muscles [Stitz (1926), Dufour (1841)]. The inner surface is closely covered with silky brown hairs which project horizontally into the lumen. Each hair is colourless at its free end, darker in the middle and light again at its root. The hairs are in serial rows on the wall of the proventriculus, Loew (1848).

The proventriculus opens into the comparatively long mid gut or mesenteron (m) which extends from the mesothorax to the anterior part of the fifth abdominal segment. The walls of the mesenteron are distensible and are studded all over externally with minute papillae, which have the appearance of small circles. The mid gut narrows posteriorly, and shortly before its junction with the hind gut arise the six malpighian tubules (mp). At the point of origin of each malpighian tubule the inner surface of the gut is raised into a papilla and from this papilla a longitudinal sinuous fold runs posteriorly to the constriction at the junction of the mid and hind gut.

The malpighian tubules coil over the posterior part of the mid gut and over the hind gut and are held by fine tracheae. They are dark red for the greater part of their length, but are colourless near their point of origin. They end freely in the abdomen.

The hind intestine is divisible into three regions. The first part is a narrow duct, which forms a large loop in its middle region—it is situated in the fifth and sixth abdominal segments. This narrow duct expands in the sixth segment into the rectum, which contains in its wall six cone-shaped rectal papillae (rg). The base of each cone is visible externally, but the apex projects into the lumen of the rectum. These glands or papillae are supplied by fine tracheae. Mercier (1920a) has described these papillae and their histology. They are very similar in their mode of development and structure to those found throughout the Diptera and Aphaniptera, and are probably important for the conservance of water as suggested by Wigglesworth (1932).

Below the rectum the hind intestine becomes very narrow as it passes through the constricted terminal segments of the abdomen. The anus opens on the eleventh segment.

The salivary glands (figs. 8, 8a).

Brants (1839), Dufour (1841) and Brauer (1855) showed that the salivary glands exhibit considerable sexual dimorphism. Those of the male are large,

while those of the female are very small. The work of these authors was unknown to or ignored by the authors succeeding them, until Mercier (1916) published his observations on the part played by the male salivary glands in mating. In a later paper Mercier (1920b) showed that the functional activity of the salivary glands of the males coincides with the end of spermatogenetic evolution. The hypopharynx of the male is scoop-shaped; it is concave on the smooth dorsal surface, but is very hairy on the convex ventral surface. The salivary duct opens at the base of the hypopharynx on its ventral surface and just posterior to the hypopharynx a pair of lateral muscles attach the salivary duct to the labium. The duct expands into a muscular-walled chamber which is supported on its ventral surface by a cuticularised plate, the limits of which are rather indefinite. This muscular chamber is followed by a smaller membranous walled sac, out of which leads the common salivary duct (sc).

The common duct passes up the rostrum to the suboesophageal ganglion, below which it divides. Each branch is expanded into a sac, out of which pass tubular glands, usually 3 in number (sg). These salivary sacs are frequently pressed together, so that the six glands appear to arise from a common chamber.

The tubular glands lie on and around the intestine and extend as far down the abdomen as the testes which are in the sixth segment. Here the free ends of the glands bend upwards. The glands are of considerable size, often as thick as the oesophagus.

The number of glandular tubes varies greatly. The normal number is six, three on either side, but specimens have been found with seven, four on one side and three on the other; others with eight, and one with nine glands, of which five were on one side and four on the other. The cause of this irregularity is not known. Mercier (1916) describes how the males emit a pearl of saliva which attracts the female; while she is eating it, the male copulates with her. I have watched the males and females together and have never seen the drop of saliva. This was probably because the insects were given plenty of food, in the form of small pieces of meat, so that it was unnecessary for the male to use his saliva to attract the female.

The salivary glands of the female consist of a pair of small sac-like tubes which project a short distance into the prothorax. They unite below the suboesophageal ganglion to form a thick common duct opening on the hypopharynx. The anterior chamber, which is found in the male, is absent and there is no supporting sclerite, but there is a small ventral plate pigmented at its apex.

The nervous system (figs. 17a, b).

The nervous system of the genus has been described by Loew (1848) and by Miyake (1913). All later descriptions, Stitz (1926) and Imms (1934), seem to have been taken from Miyake's paper. Neither description is accurate as the dissections were of females only, and it was not realised that the number of abdominal ganglia differs in the two sexes—providing a further instance of sexual dimorphism in *Panorpa*.

The brain is large and lies transversely in the dorsal part of the head (fig. 19). It expands laterally into the large optic lobes. The antennary lobes lie on the anterior surface of the brain (al) and the three large pink ocelli lie on its dorsal surface in the form of a triangle (oc). The para-oesophageal connectives are relatively short and unite the brain with the suboesophageal ganglion (sg), which is held in place by the tentorium. The dorsal surface of the suboesophageal ganglion has a shallow groove for the reception of the oesophagus.

The three thoracic ganglia are large and are connected by double commissures. The metathoracic ganglion innervates the spiracles of the first abdominal segment in addition to those of the metathorax.

The number of abdominal ganglia differs in the two sexes. In the female, the first abdominal ganglion lies close to that of the metathorax in the anterior part of the first abdominal segment. The second lies in the posterior region of the second segment, the third in the fourth segment and the fourth to the sixth ganglia in the succeeding segments, so that the sixth and last ganglion lies in the seventh segment over the junction of the oviducts. The first abdominal ganglia innervates the second abdominal spiracle, the second ganglion the third spiracle and so on. The sixth ganglion supplies the seventh and eighth spiracles.

The males of *P. communis* L. and *P. germanica* L. possess seven abdominal ganglia connected by double commissures (fig. 17b). The seventh ganglion lies in the eighth abdominal segment, beneath the vasa deferentia, and sends nerves into the fused basal lobes of the gonopods, to the ejaculatory sac, etc.

The stomodaeal sympathetic nervous system (fig. 11).

The frontal ganglion (f) lies in the notch of the sclerotised hoop (pl) of the pharynx and just anterior to the brain. One nerve runs forwards from it down the proboscis and another posteriorly along the dorsal surface of the pharynx and oesophagus. The latter is the recurrent nerve. The frontal ganglion is joined to the brain by two lateral nerves, the frontal ganglion connectives. Immediately posterior to the brain the recurrent nerve expands into the occipital ganglion (og), which is deeply grooved, indicating that it originated from a pair of ganglia. Two nerves pass posteriorly from the occipital ganglion. They lie side by side on the dorsal surface of the oesophagus, but diverge on reaching the proventriculus. At the base of the proventriculus the nerves branch several times and run on to the surface of the mid gut.

The recurrent nerve is closely associated with the aorta (ao).

The dorsal vessel extends from the pharyngeal hoop to the posterior part of the abdomen, where it terminates in the region of the hind gut. The dorsal vessel consists of two parts; the aorta, which extends from the pharyngeal hoop to the base of the metathorax, and the heart, which lies in the abdomen. The aorta opens on the pharyngeal hoop and is closely associated with the recurrent nerve which it overlies. The aorta widens above the oesophageal ganglion, contracts again posteriorly to it and then loses its connection with the nerve (rn). The aorta passes through the thorax as a very fine tube lying above the gut. In the metathorax it suddenly expands into the heart which is a wider tube of almost uniform diameter. There are usually no evident constrictions into chambers, although slight constrictions are sometimes noticeable. On either side of the heart is an irregular strand of cells, many of which are binucleate; they extend into the thorax as a single row on either side of the aorta; these cells are the dorsal or pericardial nephrocytes.

The male reproductive organs (figs. 22, 23).

The male reproductive organs have been described inaccurately by Dufour (1841), but also by Brants (1839), Brauer (1855), Loew (1848), Miyake (1913) and by Stitz (1908 and 1926). This last author described them in detail. Loew described the organs, but was unable to determine the openings of the accessory glands. My observations on *P. communis* L. and *P. germanica* L. do not agree with Miyake's description of *P. nipponensis* Nav. The following description is from my own dissections.

The testes are found in the 6th abdominal segment, their apices projecting into the 5th. Each testis consists of three elongate follicles (fe), each of which is narrowed and slightly hooked at the anterior end. The three follicles are contained in a common covering or capsule, which is of a pinkish-brown colour (ca). The follicles of each testis unite at their posterior ends to form a fine duct, the vas deferens (vd). This duct is coiled like an elongate watch spring, within the common testicular covering and is pressed against the base of the testis on the outer side, forming an epididymis (e). The duct emerges from the capsule and runs posteriorly for a short distance into the 7th segment, then it turns anteriorly to enter the vesicula seminalis (v) at its anterior end. The vesiculae seminales lie ventral to the testes in the 6th segment; they are elongate white tubes, as long but not as wide as the testes. They appear to unite at their apices, just anterior to the entrance of the vasa deferentia. Each vesicula seminalis has at its anterior end two terminal accessory glands (ac), the inner of which is inclined towards the corresponding gland of the other vesicle. The outer glands are smaller. Although these glands are very small in *P. communis* L., they are relatively long in *nipponensis* Nav. according to Miyake (1913), and are probably accessory glands.

Posteriorly the two vesiculae seminales separate slightly from one another and constrict into fine ducts, which run through segments 7 and 8 closely applied to each other and ventral to the hind intestine. They enter the chamber formed by the fused gonopods and there separate from each other, and, turning ventrally, expand slightly before they enter the large ejaculatory sac (ejs). This sac has very thick walls and a small lumen. The ejaculatory sac swells out posteriorly into a pair of large dorsal lobes, which also have thick walls and small lumina. There is a very short ductus ejaculatorius (ej), the dorsal wall of which is formed by the base of the dorsal sclerite of the aedeagus. Two muscles pass through the loop formed by the separation of the vasa deferentia and are attached to the dorsal wall of the fused basal lobes of the gonopods. These muscles unite ventrally to form a ligament which passes between the lobes of the ejaculatory sac and is attached to the dorsal sclerite. The two accessory glands (ac) lie one on either side of the ejaculatory sac. They are coiled slightly and open, on the membrane at the base of each paramere, into the cavity, enclosed ventrally by the parameres and dorsally by the forked penis.

A testis with six follicles was found in one insect.

The female reproductive organs (figs. 34, 35, and 35a).

The ovary of *Panorpa communis* L. consists, according to Gross (1903), " of a series of polytrophic ovarioles, in which each nutritive chamber contains three nutritive cells. The egg chambers and nutritive chambers are only limited externally by small constrictions."

The number of ovarioles in each ovary has been definitely stated by a number of authors. Loew (1848) recorded twelve in each ovary in *P. communis* L., while Stitz (1908) and Gross (1903) state equally certainly that there are ten ovarioles in each ovary in that species. Miyake (1913) gave the number of ovarioles in *Panorpa nipponensis* Nav. as ten. In my experience the number is variable, varying not only from specimen to specimen of the same species, but also in each ovary of the same pair of ovaries. Specimens of *P. germanica* L. possessing ten ovarioles in one ovary and eleven in the other are frequently found. In *P. communis* L. the number has been found to vary from fourteen in one ovary and twelve in the other to ten and eleven as in *P. germanica* L.

The ovarioles open on either side into the anterior part of the lateral oviduct,

in which the eggs collect before emergence. . . The lateral oviduct lies on the outer side of the ovary. The apices of the ovarioles point inwards and anteriorly towards those of the other ovary. The terminal filaments of the ovarioles of each ovary unite to form the ovarial ligament which joins that of the other ovary in the median line. The position and shape of the ovary depends largely on its maturity. When the insect is mature the anterior part of the lateral oviduct will be swollen with mature oocytes, while the ovarioles will be insignificant.

The lateral oviducts (ov) unite in the posterior region of the sixth abdominal segment to form the oviductus communis or common oviduct (co) which passes through segments 7–9 and opens into the ventral region of the genital chamber.

The dorsal accessory glands (ac) consist of a pair of long, thick, much coiled tubes, which generally lie on either side of the intestine and extend forwards into the 1st abdominal segment. They lie below the ovaries for the greater part of their length, but they pass dorsally in the 5th abdominal segment and in the middle of the 6th they unite to form a common duct (acd) which lies in the median line between the lateral oviducts. This duct is much finer than the glands themselves. It rises over the junction of the lateral oviducts to run posteriorly along the dorsal surface of the common oviduct. It is rather longer than the latter and is therefore coiled here and there in its length.

The spermatheca (sp) [the seminal vesicle of Loew (1848) and the bursa copulatrix of Stitz (1908)] lies in the anterior region of the 6th segment between the oviducts, with fat body clinging closely to it. When the fat body has been removed it is found that the spermatheca is largely thin walled. It is shaped like an oval capsule, the tip of which has been bent posteriorly and held in this position by muscles attached anteriorly to the tip and posteriorly two-thirds of the way down the capsule. The shape of the capsule varies with the species. The base of the capsule is opaque and a thick-walled tube with transversely wrinkled walls leads from it. The thick-walled tube narrows to form the very fine spermathecal duct (spd), which runs over the sixth abdominal nerve ganglion, which lies in the fork of the oviducts. It then follows a course along the dorsal surface of the common oviduct, lying immediately below the common duct of the accessory glands, until it reaches and enters the spermathecal rod (spr). This rod is called the " internal skeleton " by Miyake (1913) and Issiki (1933). It lies in a pocket of the intersegmental membrane between segments 9 and 10. The spermathecal duct is considerably longer than the common oviduct and is therefore much coiled in its progress. It is of uniform fineness and enters the anterior end of the spermathecal rod, the point of entrance varying with the species. The duct passes through the rod and opens at its bulb-like apex into the genital chamber.

In *P. communis* L. the duct enters the rod at its apex between the two Y-shaped arms (spa), but slightly ventral. The rod of *P. germanica* L. is only slightly broadened at its proximal end, the arms diverge hardly at all, and the duct enters the rod on the ventral surface a short distance from the anterior end (fig. 35a). The ventral surface of the spermathecal rod is less strongly cuticularised than the dorsal, in both species, so that at the distal end of the rod the duct can be seen within it, through the membrane which covers it. The distal end of the rod is covered ventrally by a muscular cap at the apex of which the duct opens (spo).

This description differs from that of Stitz (1908, 1926) which states " that the duct of the ' bursa copulatrix ' expands into a vesicle, the receptaculum seminis, out of which two ducts lead. The ventral and larger duct lies along the

surface of the oviduct, while the dorsal and finer duct enters the rod of the internal skeleton (spermathecal rod)."

I have come to the conclusion after numerous dissections of *P. communis* L. and *P. germanica* L. that Stitz confused the " expansion of the receptaculum seminis " with a small median accessory gland (acm), lying on the dorsal surface of the common oviduct, but ventral to the spermathecal duct. This gland (figs. 34 and 35) is sac-like; its size varies from specimen to specimen, but it is always small. Its proximal end lies a short distance anterior to the spermathecal rod and its wide duct lies ventral to the rod and opens on the intersegmental membrane forming the genital pouch, immediately ventral to the point where the spermathecal rod enters the spermathecal pocket (fig. 35, spp). This pocket is the " basal plate " of Issiki (1933).

Stitz seems to have been depending largely on sections for his interpretation of this part of the anatomy, and he has mistaken this accessory gland, in his sections, for the continuation of the spermathecal duct. His " ventral duct " corresponds to the duct of the accessory gland, while his " dorsal duct " is the true spermathecal duct which runs through the rod.

The common oviduct, spermathecal duct and the ducts of the two accessory glands open to the exterior by separate openings on a much-folded membrane, which forms the wall of the genital pouch and which is the intersegmental membrane between segments 9 and 10.

Snodgrass (1933) considered this genital pouch to be an invagination of the body wall and to correspond with the genital chamber of more generalised insects. Unlike the latter, it is closed below by the 9th sternum and not the 8th as is usually the case. This pouch functions as the bursa copulatrix.

The external openings of the reproductive organs have never been described.

The membrane connecting the 10th sternite with the 9th and forming the genital chamber is very much folded and the openings of the genital system occur in definite relation to these folds. The diagram (fig. 42) represents a median longitudinal section of the 9th and 10th segments. The membrane passes anteriorly from the 10th sternite into the 9th segment, where the duct of the dorsal accessory gland (acd) opens on to it in the median line. The membrane continues anteriorly and then folds ventrally and passes posteriorly in the mid line only, where it is pushed out into a deep posteriorly directed pocket (spp) by the spermathecal rod (spr). This pocket is the spermathecal pocket and is produced laterally into a wing or process on either side (spw), which is cuticularised on its ventral surface. Dorsally the membrane of the pocket is stretched between the processes, but ventrally the wall is pressed out into a hollow in which the spermathecal rod lies.

The muscles from the arms of the spermathecal rod are attached to the intersegmental membrane a little posterior to the opening of the spermathecal pocket.

The wings (spw) and the part between them are the " distal plate " and the " apical processes " of Issiki (1933) and the " wings of the cone " of Stitz (1908). The anterior part of the pocket surrounding the spermathecal rod corresponds to the basal plate of Issiki (1933). The posterior end of the spermathecal rod is fused to the membrane of the pocket and the spermathecal duct opens on it (spo). Around and behind the spermathecal pocket (spp) the intersegmental membrane again bends posteriorly, and just where it turns over and in the median line is the opening of the median accessory gland (acm). The membrane then passes posteriorly and is continuous with the 9th sternite. Immediately below the end of the spermathecal rod, the common oviduct opens on to the

intersegmental membrane. The membrane on either side of this opening is thrown into a protecting fold. In front of the opening is a cavity into which the bulb of the spermathecal pocket can fit and so effectively close the opening of the common oviduct, and control the fertilisation of the egg. The membrane on either side of the spermathecal pocket forms the back and sides of the genital chamber and is also attached by muscles to the overlapping 9th tergite.

Terminal segments of the female abdomen.

Miyake (1913) stated that in *P. nipponensis* Nav. the 9th sternite or subgenital plate is subtriangular in form and is composed of two spindle-shaped plates connected by membrane. In *P. germanica* L. there is no indication of the two plates, except on the anterior region of the sternite, where there is a median emargination of the anterior margin, which is continued as a median band free of bristles for about half the length of the sternite. In *P. communis* L. the emargination of the margin is reduced and there is little or no sign of the clear band. This difference between *P. nipponensis* Nav. and the British species is of interest when one considers the condition obtaining in *Boreus hyemalis* L., which is described later.

A comparison of the internal organs of *Brachypanorpa carolinensis* Banks, *Chorista australis* Klug, *Boreus hyemalis* L., *Merope tuber* Newm., *Bittacus pilicornis* Westw., *Harpobittacus tillyardi* Esben-Peters., and *Apterobittacus apterus* McL. with those of *Panorpa.*

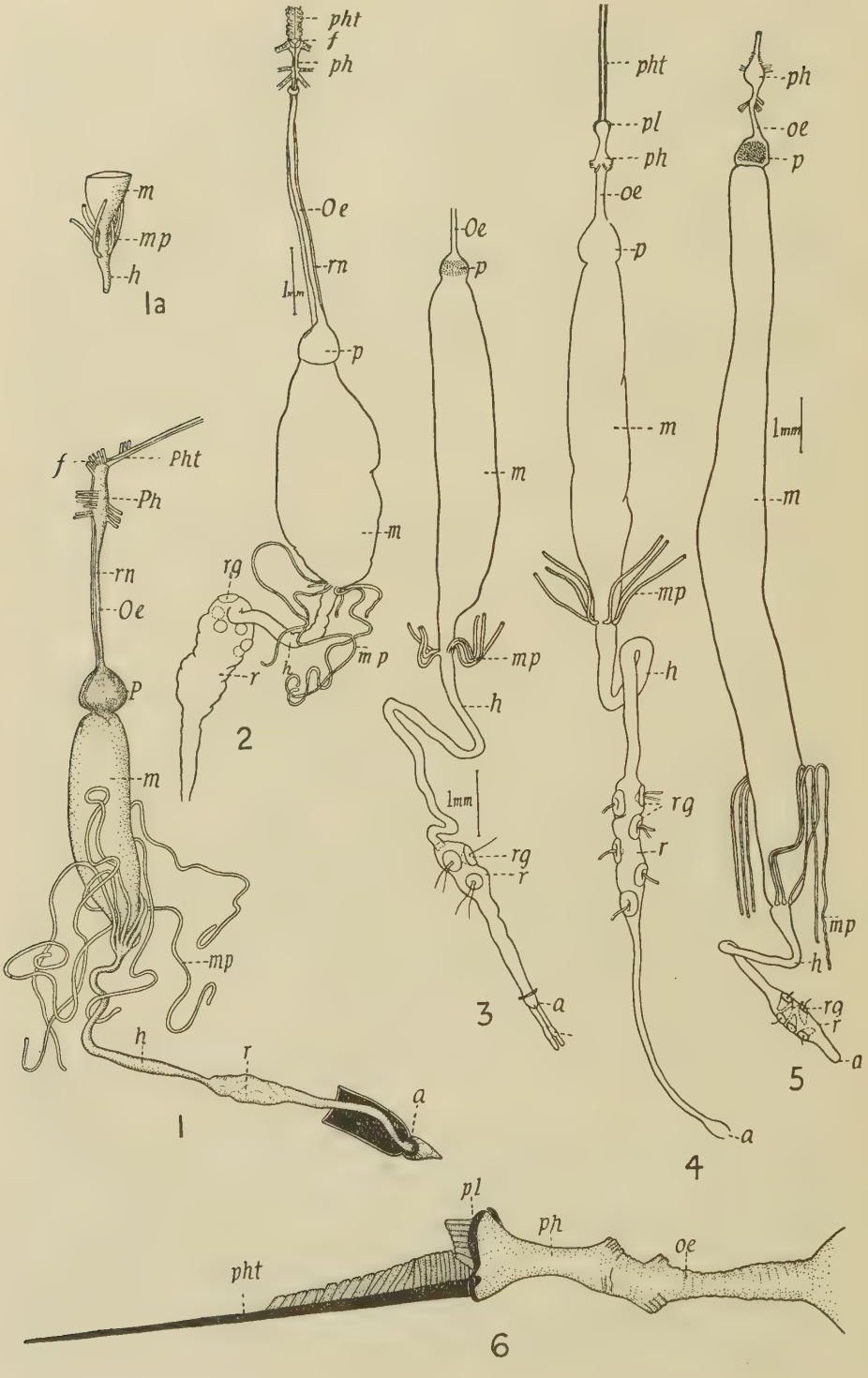
Alimentary canal.

Brachypanorpa carolinensis Banks. The pharynx and proventriculus are similar to those of *Panorpa.* The proventriculus lies in the anterior part of the prothorax and the mid gut extends into the 4th abdominal segment, where it is abruptly constricted. It receives the six malpighian tubules and enters the narrow, coiled hind gut. The latter passes into the large, thin-walled rectum in the same segment. The rectum extends from the posterior region of the 4th segment into the 11th segment on which it opens. There are six rectal papillae.

Chorista australis Klug (fig. 3). The oesophagus is short and the proventriculus is of the Panorpoid type. The mid gut is long and sac-like and the six malpighian tubules arise at its junction with the hind gut, in two groups of three. The first part of the hind gut has a deep S bend; there is a valve between it and the rectum, the second part of the hind gut, which contains six well-developed rectal papillae. Below the papillae the hind gut becomes very narrow and opens on the eleventh segment.

Boreus hyemalis L. (fig. 1), Brauer (1855) gave a brief description of the alimentary canal; Withycombe (1921) and Stitz (1926) make slight mention of it.

The pharynx consists of a long, narrow cuticularised trough (pht) covered dorsally by membrane, which is continuous forwards as the epipharynx. Anterior to the brain, the pharyngeal trough ends in two short lateral arms. Muscles connect the membranous roof of the pharynx to the inner surface of the frons and clypeus. These muscles are quite short, because the pharynx lies in a dorsal position in the proboscis. Strong muscles are attached to the lateral arms of the trough and to the wall of the oesophagus behind it, which pass to the tentorium and wall of the head. Between these muscles, on the dorsal surface of the pharynx, lies the frontal ganglion (f). As it passes through the nerve ring, the canal expands and the strongly muscular walls are supported by lateral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muscles attached to the tentorium. The muscular chamber contracts into a narrow oesophagus, which passes backwards into the thorax, where it expands into the large proventriculus (p). This is bluntly cone-shaped and not spherical as stated by Stitz (1926). Its structure is similar to that of *Panorpa*.

The mid gut is sac-like and comparatively short, being little longer than the oesophagus. At its posterior end it narrows into a thin tube, which expands again shortly before the origin of the malpighian tubules. There are six of these, placed close together on the ventral and lateral parts of the canal, leaving a small clear area on the dorsal surface. They are long and slender, of uniform thickness and end freely in the body cavity.

The hind intestine narrows and coils slightly in the abdomen and enlarges again into the rectum, the walls of which are strongly muscular. The anterior region is sac-like, but the posterior is narrow and tubular and opens on the 10th segment in the male and on the 11th in the female. The hind gut of the female is longer than that of the male, because it has to traverse the long terminal segments of the abdomen. The wide muscular rectum is homologous with that part of the gut of *Panorpa* which bears the rectal glands. These glands are entirely absent in *Boreus*. The inner surface of the rectum is thrown into transverse folds projecting into the lumen of the canal. No tracheae are especially associated with this part of the gut as they are in *Panorpa*.

Merope tuber Newm. (fig. 2). The pharyngeal trough is short and the pharynx is not swollen or muscular. The oesophagus is relatively long and the proventriculus is similar to that of *Panorpa*. The mid gut is sac-like and no longer than the oesophagus and the six malpighian tubules are symmetrically arranged around the junction of the mid and hind gut. The hind gut shows the same three areas as in *Panorpa*; the six rectal papillae are grouped at the anterior end of the rectum and are smaller than those of *Panorpa*. The position of the hind gut in the male differs from that of the female, owing to the short body and enormous gonopods of the former. It lies below the testes and emerges on the right side of the abdomen, then runs across the abdomen, posteriorly to the testes and expands into the rectum, which lies in the base of the left gonocoxite (fig. 29). The rectum narrows and passes into the mid line of the abdomen, where as a wide, short tube it opens on the 10th segment between the gonocoxites.

Bittacus pilicornis Westw. (fig. 5). Brauer (1855) described briefly the alimentary canal of *B. tipularius* Latr. (*italicus*).

The pharyngeal trough is short, because although the head appears to be elongate, this appearance is produced by the free mouthparts, which are relatively much longer than those of *Panorpa*. The arms of the posterior end of the trough embrace the muscular pharyngeal chamber. The oesophagus is short and the proventriculus, which is similar to that of *Panorpa*, lies in the anterior part of the prothorax. The mid gut is a wide tube which extends into the posterior part of the 7th segment. The six malpighian tubules are arranged in two groups of three; at the base of each tubule is a small globular swelling.

FIGS. 1–6.—Alimentary canal of Mecoptera. 1. *Boreus hyemalis* L. ♀; 1a. *Boreus hyemalis* L. ♀, showing arrangement of malpighian tubules; 2. *Merope tuber* Newm.; 3. *Chorista australis* Klug ♀; 4. *Panorpa communis* L. ♀; 5. *Bittacus pilicornis* Westw. ♀; 6. *Panorpa communis* L., pharynx and pharyngeal trough.
a, anus; f, frontal ganglion; h, hind intestine; m, mid gut; mp, malpighian tubules; oe, oesophagus; p, proventriculus; ph, pharynx; pht, pharyngeal trough; pl, lateral arms of pharyngeal trough; r, rectum; rg, rectal glands; rn, recurrent nerve.

The tubules run forward into the 6th segment and then back towards the hind gut. The three parts of the hind gut are present as in *Panorpa*; the first part makes an S bend and the rectal sac is almost filled by the six large rectal papillae. The anus lies on the 11th segment in the female.

Apterobittacus apterus McL. ♂. The pharynx is very similar to that of *Bittacus*. The oesophagus is short and opens into the proventriculus in the anterior part of the prothorax. The proventriculus is long oval in shape and not wider at the base as is that of *Bittacus*. It is similarly lined with golden brown hairs projecting into the lumen. The oesophageal valve is present. The mid gut is a wide straight tube, which extends from the prothorax into the middle of the 6th abdominal segment. The six malpighian tubules are arranged in two sets of three as in *Bittacus* (fig. 5, mp.), but their bases are not swollen. The three parts of the hind gut resemble those of *Bittacus*. The anterior curve of the S bend lies against the base of the testes. As in *Bittacus*, the six rectal papillae almost fill the rectal sac. The rectum narrows below the sac.

Salivary glands.

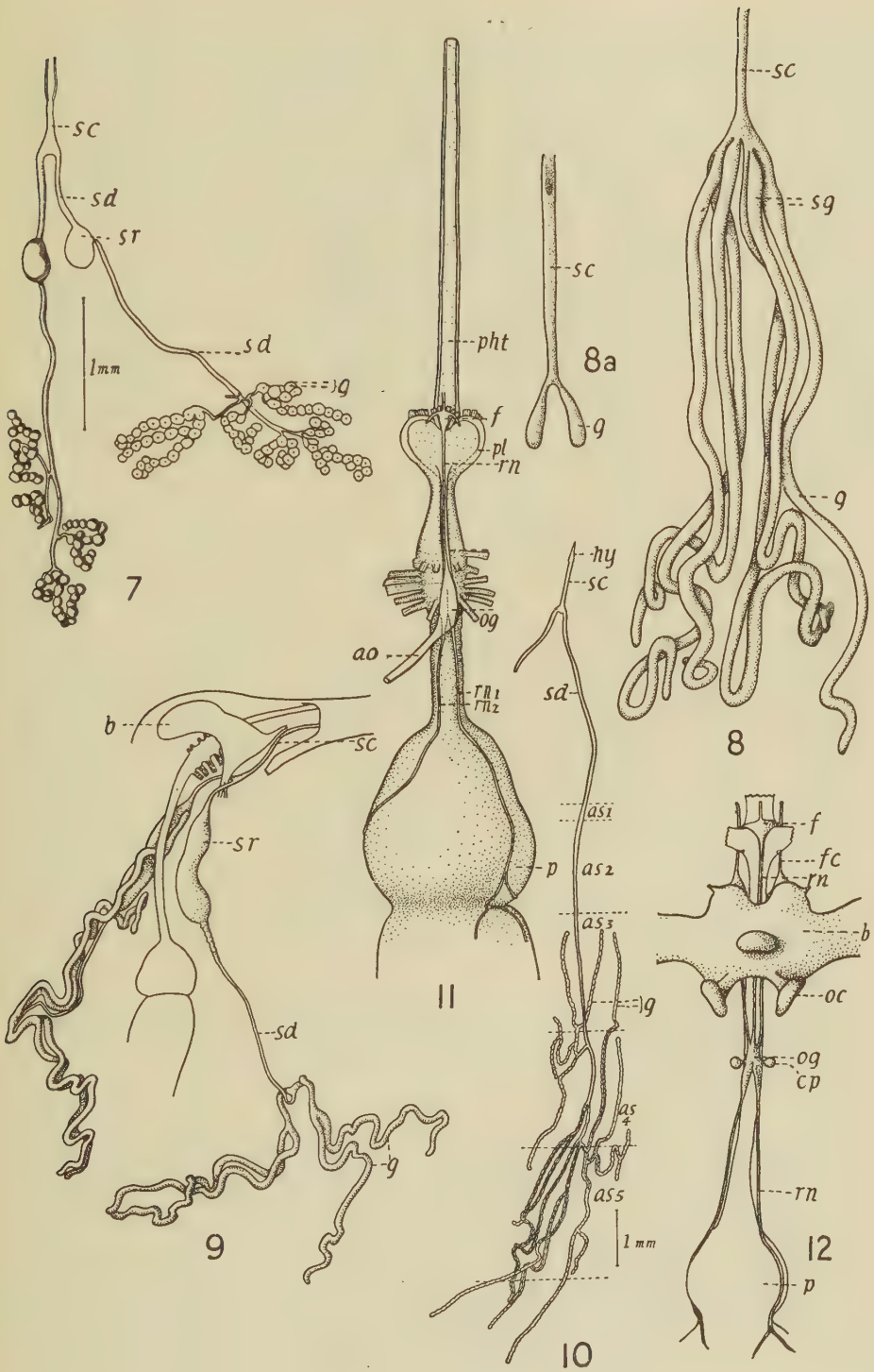
Brachypanorpa carolinensis Banks. The short common duct of the salivary glands divides below the suboesophageal ganglion just anterior to the tentorium. A branch runs on either side of the nerve cord and in the prothorax breaks up into what appear to be large-celled lobules; unfortunately the gland was unrecognisable owing to its bad state of preservation.

Chorista australis Klug. The structure of the glands was not recognisable in the material available. A common salivary duct is present in the head.

Boreus hyemalis L. (fig. 9). The ventral surface of the hypopharynx is strongly sclerotised and this is continued forward to form a " toecap " over its anterior end. The fine salivary duct opens at the posterior end of the sclerite and rises dorsally from its ventral position on the labium to lie under the pharynx. It remains in this position until it reaches the suboesophageal ganglion in the head, under which it passes. At the junction of the head and prothorax the duct divides. The branches run one on either side of the nerve cord, but dorsal to it and very shortly expand into thin-walled sacs or reservoirs (sr). The duct leading from the reservoir is very much wrinkled and becomes finer and finer as it passes posteriorly. In the region of the mid gut the ducts enter the salivary glands (sg). Fig. 9 shows the duct and gland of the left side in their natural positions, while those of the right side are spread out. Each gland consists of two short tubes, each of which divides into two rather long tubules—four tubules in all. Two of the tubes are closely applied to the duct and reservoir of their side; the other two tubes lie close to the gut. The structure of the glands is similar in the two sexes and in this respect differs considerably from *Panorpa*.

Figs. 7–12.—Salivary glands and stomodaeal sympathetic nervous system. 7. *Merope tuber* Newm. ♀, gland of right side in section, showing the nuclei of the gland cells; 8. *Panorpa communis* L. ♂, normal gland; 8a. *Panorpa germanica* L. ♀; 9. *Boreus hyemalis* L. ♀, gland of left side in normal position, that of right dissected out; 10. *Bittacus pilicornis* Westw. ♂, gland of right side; 11. *Panorpa communis* L. ♀, stomodaeal sympathetic nervous system; 12. *Chorista australis* Klug ♂, Stomodaeal sympathetic nervous system.

as, abdominal segment; ao, aorta; b, brain; cp, corpus allatum; f, frontal ganglion; fc, frontal ganglion connectives; g, salivary gland; hy, hypopharynx; oc, ocellus; og, occipital ganglion; rn_1, rn_2, branches of recurrent nerve; rn, recurrent nerve; sc, common salivary duct; sd, salivary duct; sr, salivary reservoir.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Merope tuber Newm. (fig. 7). The hypopharynx is triangular in shape and fleshy. The apical opening is protected by a definite dorsal and ventral lip. Just behind the hypopharynx the duct is strengthened by a ventral cuticular plate. The short common duct widens into a triangular sac, from the basal angles of which the salivary ducts emerge. These run posteriorly and enter two pea-like sacs (sr). The sacs are dorsal, the ducts enter them apically and slightly ventrally, and about midway down the sac the duct emerges as a wrinkled tube. The ducts continue posteriorly on either side of the oesophagus and branch, giving rise to a varying number, about seven, of short chains of globular cells. The glands of the male and female are similar.

Bittacus pilicornis Westw. (fig. 10). The hypopharynx is long and triangular. The common salivary duct lies below the pharyngeal trough and bifurcates below the suboesophageal ganglion. Each branch duct lies close to the oesophagus. The gland consists of several dichotomously branching tubules opening into the duct in an irregular way. Each tube is constricted so that it has the appearance of a chain of cells, through which runs a fine duct. The number of ultimate branches varies; in one female there were fourteen, and in a male there were sixteen. The longer branches of the gland extend into the 6th segment. There does not seem to be any sexual dimorphism.

Harpobittacus tillyardi Ebsen-Peters. is similar to *Bittacus pilicornis* Westw.

Apterobittacus apterus McL. ♂. The hypopharynx is similar to that of *Bittacus*. The common salivary duct is constricted where it opens on the hypopharynx, but immediately expands into a tube of wide lumen resembling that of *Panorpa* ♂ (fig. 8, sc) rather than that of *Bittacus* (fig. 10, sc). It branches below the suboesophageal ganglion and the ducts rise up on either side and are pressed close together over the nerve connectives as they pass through the occipital foramen and under the tentorial bridge. The ducts then diverge and lie on either side of the oesophagus. They enter the swollen ends of the salivary glands in the anterior part of the prothorax. The glands gradually narrow, but remain thicker than their ducts. They lie above and on either side of the mid gut. In the second abdominal segment they bifurcate, after which each branch bifurcates irregularly. It was not possible to follow the branching owing to the poor state of preservation of the material. The glands extended into the 6th abdominal segment. The branching is similar to that of *Bittacus* (fig. 10, g), although all the branches are directed posteriorly, but the consistency and structure bear more resemblance to those of *Panorpa* male (fig. 8, sg).

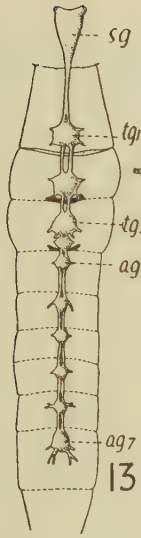
Central nervous system.

Brachypanorpa carolinensis Banks. The central nervous system of the male is similar to that of *Panorpa* ♂, except that the connective between the suboesophageal and prothoracic ganglia is single instead of double.

Figs. 13–21.—Central nervous system. *13. *Boreus hyemalis* L. ♀; 14. *Boreus hyemalis* L. ♂, brain; 15a. *Merope tuber* Newm. ♂; 15b. *Merope tuber* Newm. ♀; 16a. *Bittacus pilicornis* Westw. ♂; 16b. *Bittacus pilicornis* Westw. ♀; 17a. *Panorpa communis* L. ♀; 17b, *Panorpa communis* L. ♂; 18a. *Chorista australis* Klug ♀; 18b, *Chorista australis* Klug ♂; 19. *Panorpa communis* L., brain; 20. *Bittacus pilicornis* Westw. ♂, brain; 21. *Merope tuber* Newm. ♂, brain.

ag, abdominal ganglion; al, antennary lobe; b, brain; f, frontal ganglion; hy, hypopharynx; oc, ocellus; ph, pharynx; pht, pharyngeal trough; rn, recurrent nerve; sc, common salivary duct; sg, suboesophageal ganglion; sp, spiracular nerve; sr, salivary reservoir; tg, thoracic ganglion.

* Ag_2 is by error marked Ag_1.



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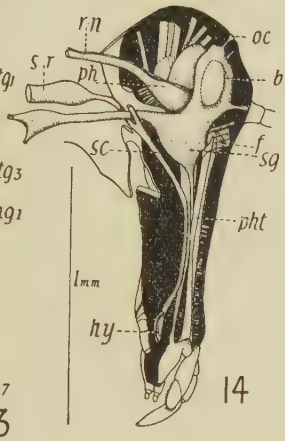

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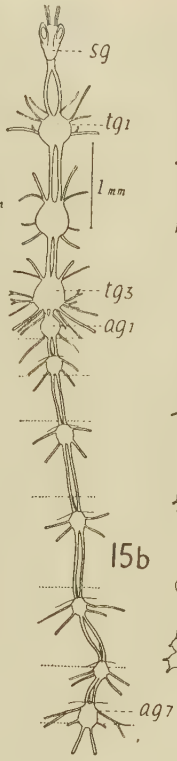

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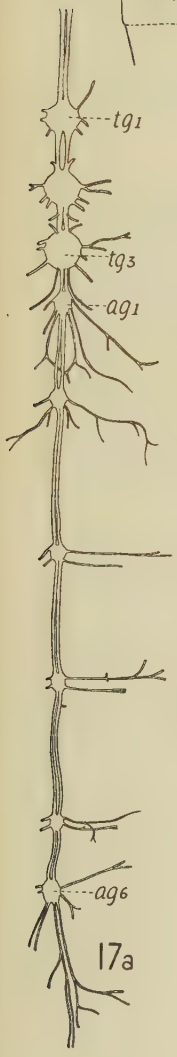

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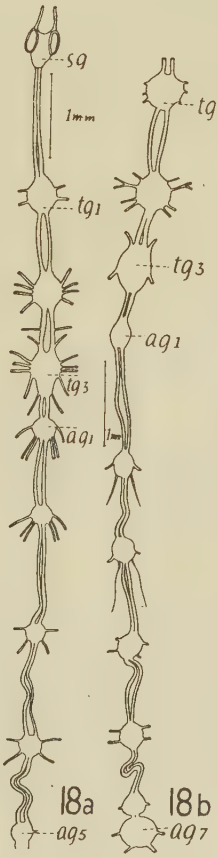

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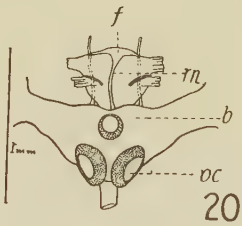

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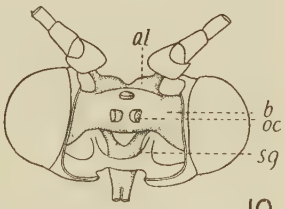

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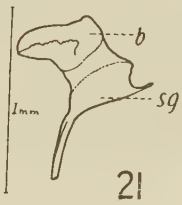

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There are seven abdominal ganglia. The nervous system of the female could not be dissected because of the state of the material, but it is probable that it is similar to *Panorpa* and possesses six abdominal ganglia.

Chorista australis Klug (figs. 18a, b). The central nervous system is similar to that of *Panorpa*. There are seven abdominal ganglia in the male and five or six (probably six as in *Panorpa*) in the female.

Boreus hyemalis L. (figs. 13, 14). The brain (b) is large and expands laterally into the large optic ganglia. Three short nerves pass dorsally to the ocelli (oc) on the vertex. The antennary lobes are small and their nerves rather fine. The para-oesophageal connectives are relatively very wide and short and the suboesophageal ganglion (sg) is deeper than it is wide and projects into the proboscis. It is held in position in the head by the tentorium. Nerves pass from the suboesophageal ganglion, down the proboscis, to the mouthparts. The connectives between the suboesophageal ganglion and the prothoracic ganglion are fused for almost their entire length, separating only just in front of the prothoracic ganglion, but the connectives joining the remaining ganglia are double. There are three large ganglia in the pro-, meso- and metathoracic segments respectively, and seven abdominal ganglia (see also Brauer 1855, female). The first abdominal ganglion lies in the metathorax joined by very short connectives to the metathoracic ganglion. The remaining six ganglia lie in abdominal segments 1 to 6, but the 7th ganglion is larger than the others. The number of ganglia is similar in the two sexes.

Merope tuber Newm. (figs. 15a, b). The brain is very similar to that of *Boreus*. The connectives between the brain and the suboesophageal ganglion are short and wide, so that the oesophagus appears to be passing through a hole in the brain. The suboesophageal ganglion is narrow, but is produced forwards, as are also the para-oesophageal connectives. Anteriorly and above the connectives are the small antennary lobes. The first thoracic ganglion is grooved longitudinally for the reception of the oesophagus. The first abdominal ganglion lies in the metathorax, but innervates the first abdominal segment. The second ganglion lies in the first segment, but supplies the second; the remaining ganglia lie in their corresponding segments.

There are eight abdominal ganglia in the male; the last three are joined by very short connectives, due to the telescoping of segments 7 and 8 into 6.

There are seven abdominal ganglia in the female.

Bittacus pilicornis Westw. (figs. 16a, b, 20). Brauer (1855) briefly described the nervous system of *B. tipularius* Latr. (*italicus*). He found seven abdominal ganglia but did not state the sex of the insect.

The brain is wide and carries the three stalked ocelli on its dorsal surface. The para-oesophageal connectives are short and the suboesophageal ganglion is grooved for the oesophagus. The tentorial bridge overlies the connective between the suboesophageal and the prothoracic ganglia. The connectives between these ganglia are double in the female, but almost completely fused in the male.

The connectives between the pro-, and meso-, and the meso- and metathoracic ganglia are double in both sexes.

The first abdominal ganglion is fused with the metathoracic ganglion and sends nerves, which are fused with the connectives for a short distance, to the 1st abdominal segment. The connectives between the abdominal ganglia are single and only show an indication of their double nature just in front of each ganglion.

The second abdominal ganglion lies in the posterior part of the 2nd abdominal

segment and supplies the 3rd segment also. The third ganglion lies in the anterior part of segment 4, the fourth in the anterior part of 5, the fifth in the 6th segment and, in the female, the sixth, which is a compound one, lies in the 7th segment on the junction of the lateral oviducts.

There are seven abdominal ganglia in the male, the first fused with metathoracic ganglion; the connectives between 5 and 6 are double and very short.

Harpobittacus tillyardi Esben-Peters. The nervous system is similar to that of *Bittacus*, except that the abdominal connectives are double.

Apterobittacus apterus McL. The brain and suboesophageal ganglion of the male are similar to those of *Bittacus* (figs. 20, 16a), but the connectives between the suboesophageal and prothoracic ganglia are double, as are also those of the other thoracic ganglia.

There is an almost complete constriction between the metathoracic and first abdominal ganglia. The former supplies the 1st abdominal segment and the latter sends nerves to the 2nd abdominal segment. The second abdominal ganglion lies in the posterior part of segment 2 and supplies the 3rd segment; the third ganglion lies in segment 4 and supplies it. Ganglia four, five and six lie in and supply segments 5, 6 and 7. The seventh ganglion is separated by very short connectives from the sixth and lies just within the slightly invaginated segment 8 and supplies it and the following segments. The connectives between the other abdominal ganglia are single except for the posterior quarter, which is double.

The nervous system of the female is similar to that of the male, but there are only six abdominal ganglia.

There are the same number of abdominal ganglia as in *Bittacus*, but the first ganglion is more distinct and the connectives are double for a greater part of their length. *Apterobittacus* comes between *Bittacus* and *Harpobittacus* as regards the nervous system.

The stomodaeal sympathetic nervous system.

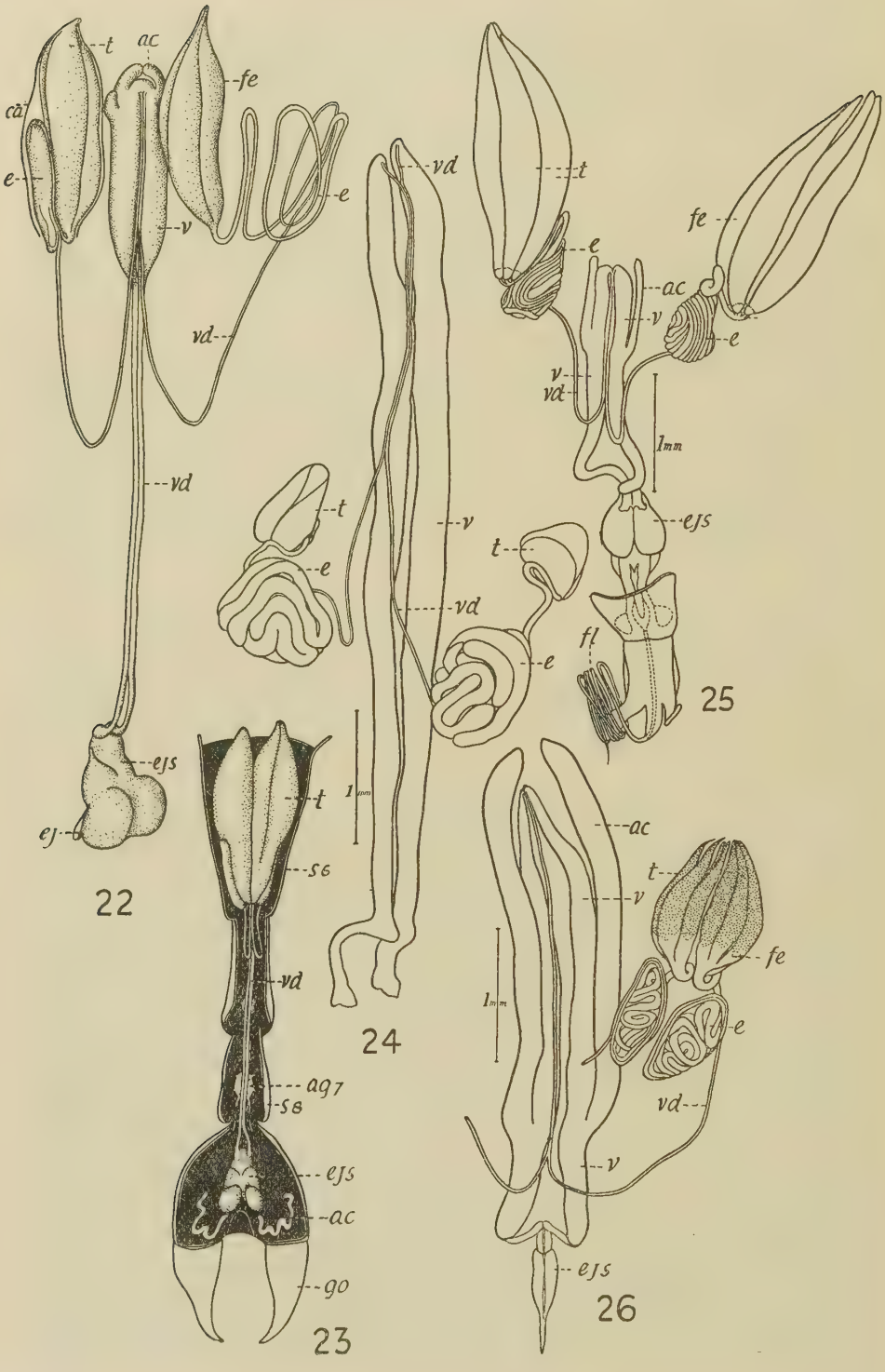
Brachypanorpa carolinensis Banks. The sympathetic nervous system is similar to that of *Panorpa*, but the branches of the recurrent nerve diverge immediately on leaving the occipital ganglia.

Chorista australis Klug (fig. 12). The frontal ganglion (f) lies between the muscles on the dorsal surface of the pharynx in front of the brain. It gives off the frontal ganglion connectives to the brain, a median anterior nerve and a median posterior nerve, the recurrent nerve (rn). The latter passes along the dorsal surface of the pharynx, below the brain, and on the oesophagus enters the occipital ganglion (og), on either side of which lie the corpora allata (cp). Two branches of the recurrent nerve (rn_1, rn_2) run along the sides of the oesophagus, over the proventriculus and break into numerous branches on the mid gut.

Boreus hyemalis L. (fig. 1). The frontal ganglion (f) lies in a similar position to that of *Panorpa*, on the pharynx, in front of the brain. The recurrent nerve (rn) runs along the pharynx and oesophagus, over the proventriculus, to branch on the mid gut. It is a single nerve and not double as in *Panorpa*. The occipital ganglion was not seen.

Merope tuber Newm. (fig. 2). This genus is similar to *Panorpa*. The recurrent nerve forks below the occipital ganglion and the two branches pass down the oesophagus to the proventriculus.

Apterobittacus apterus McL. The frontal ganglion and its connectives are similar to those of *Chorista*. The recurrent nerve runs along the dorsal surface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of the oesophagus, gradually thickening, until half-way between the brain and proventriculus it enters the two occipital ganglia which adhere in the mid line. Each ganglion sends a nerve to the brain and bears on its anterior outer margin a small globular corpus allatum, similar to *Chorista* (fig. 12). A nerve runs from each ganglion down the oesophagus and branches on the proventriculus.

Male reproductive organs.

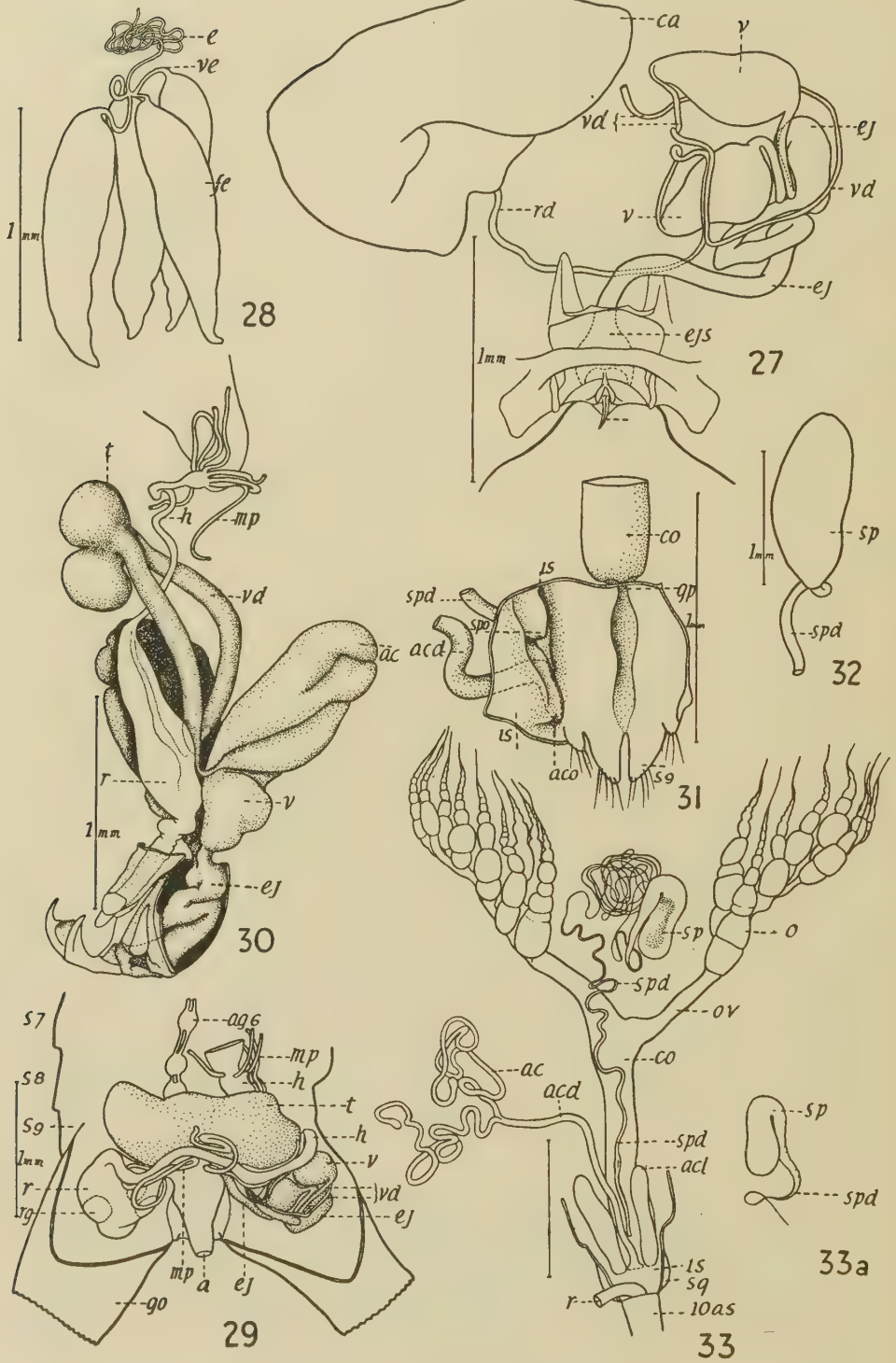
Brachypanorpa carolinensis Banks (fig. 50). The testes (t) lie in the anterior part of the 6th abdominal segment and each consists of three follicles (fe). All but the base of each follicle is dark purple in colour and the apex of each is produced into a narrow neck which ends in a rounded lobule, the follicular process (fp). The vasa efferentia are very short and thick and open into the end of the vas deferens (vd). Each testis is covered by a fine membrane (ca). The vas deferens coils into an epididymis (e), which lies in the anterior part of the 7th segment. The epididymis is also enclosed in a fine membrane. The vas deferens on leaving the epididymis after one bend, turns towards the mid line and meets the other vas deferens. The two adhere and run forwards to the apices of the vesiculae seminales (v), which they enter in the middle of the 6th segment. Two finger-like accessory glands (ac) arise dorsally on each vesicula seminalis, a short distance behind the entrance of the vas deferens. The vesiculae seminales pass posteriorly side by side into the 8th segment, where they narrow abruptly (vd) and run through the 9th segment into the fused bases of the gonopods. They diverge to enter the apex of the ejaculatory sac (ejs) laterally. The latter is a long thick-walled sac with two dorsal lobes.

Chorista australis Klug (fig. 24). The testes (t) lie in the 4th or 5th segment. In the specimen figured, one lay in the 4th and one in the 5th segment on either side of the body. Each testis consists of three small follicles (fe) closely pressed together. The vas deferens (vd) adheres to the testis for a short distance, and then passes posteriorly, for a distance which varies in different specimens, and forms a closely coiled knot or epididymis (e), which appears to be covered by a membranous envelope. The epididymis, when unravelled, consists of a thick tube gradually narrowing towards its free ends. The vas deferens emerges from the epididymis as a fine tube which runs anteriorly into the second abdominal segment where it enters the apex of the vesicula seminalis (v) of its side. The two vesiculae seminales lie in the mid line of the abdomen and extend from the 2nd segment to the posterior margin of the 8th. They then enter the bulb formed by the 9th segment and the gonopods. They appear to narrow suddenly and to enter a large common chamber as in *Panorpa*, but this is uncertain, as the chamber, in the material available, had dried and shrunk against the wall of the segment and adhered closely to the solidified muscles.

Boreus hyemalis L. (fig. 30). The male reproductive organs are described by Stitz (1926) and Steiner (1937), but their descriptions do not agree entirely with my observations. The two testes (t) are fused into a single median structure, which is constricted to form two large spherical lobes lying one above the other.

FIGS. 22–26.—Male reproductive organs. 22. *Panorpa communis* L., male organs dissected out; 23. *Panorpa communis* L., male organs in situ; 24. *Chorista australis* Klug ♂; 25. *Bittacus pilicornis* Westw. ♂, aedeagus and cut end of membrane joining the gonopods; 26. *Harpobittacus tillyardi* E.-P. ♂.

ac, accessory gland; as, abdominal segment; ca, capsule; e, epididymis; ej, ejaculatory duct; ejs, ejaculatory sac; fe, follicle; fl, flagellum; go, gonopod; s, sternite; t, testis; v, vesicula seminalis; vd, vas deferens.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29

The vasa deferentia (vd) arise laterally from the constricted area between the two lobes. They are thick-walled tubes, which run posteriorly and then narrow abruptly to enter the base of the accessory glands (ac). These are large opaque white structures with exceedingly thick walls. The lumen of the glands is thrown by deep infoldings of the walls into three divisions or pockets. Immediately posterior to the point of entrance of the vas deferens the structure is constricted and then expands into a large basal chamber, also having thick walls and a small lumen. This chamber, the vesicula seminalis (v), narrows in to a short duct which joins the other duct of the pair to form the thick walled, coiled ductus ejaculatorius (ej). The ductus lies in the median chamber between the gonopods. This chamber is bounded dorsally and ventrally by membrane. Fig. 30 shows the right-hand gonopod removed so that the ductus can be seen folded in the median chamber. During coitus the ductus can be evaginated through the apparent genital opening (gp) between the gonopods. There is no true aedeagus.

Merope tuber Newm. (figs. 27, 28, 29). The testes (t) lie in a common sac or scrotum (ca) on the dorsal surface of the hind gut in the 8th and 9th segments. The sac is roughly in the shape of a triangle and from each angle of the base emerges a vas deferens (vd). The right-hand vas deferens passes over the hind gut into the base of the right gonocoxite. The left one runs down the ventral wall of the body cavity, below the gut, and across the body, also to enter the base of the right gonocoxite. In the base of the latter appendage lies a knot of tubes consisting of the malpighian tubules (mp), which lie in the anterior part of the knot, vasa deferentia (vd), seminal vesicles (v), and the ductus ejaculatorius (ej).

The two fine vasa deferentia (vd) meet and adhere for a short distance, then separate and each enters the apex of a pear-shaped body, the vesicula seminalis (v).

The vasa deferentia emerge from the vesiculae seminales as thicker and more opaque tubes, which coil slightly and open into the swollen apex of the thick ductus ejaculatorius (ej). The latter coils twice on itself and then runs anteriorly out of the right gonocoxite to the mid line of the abdomen, where it opens into a small pouch contained in a sclerotised structure between the gonocoxites.

The opening of the ductus is protected by an upward projecting sclerite.

When the testicular sac or capsule (ca) is opened, the two testes are seen pressed together. Each testis consists of four follicles (fe), each of which opens into a short vas efferens (ve). The vasa efferentia unite and the common duct coils into a compact epididymis (e) which rests on the bases of the follicles within the testicular sac. The vas deferens leaves the epididymis and emerges from the basal angle of the sac.

FIGS. 27–33.—Male and female reproductive organs. 27. *Merope tuber* Newm. ♂; 28. *Merope tuber* Newm. ♂; testis removed from capsule; 29. *Merope tuber* Newm. ♂; reproductive organs in situ; 30. *Boreus hyemalis* L. ♂; 31. *Chorista australis* Klug ♀, genital pouch cut open to show the openings of the common oviduct, spermathecal duct and accessory gland; 32. *Chorista australis* Klug ♀, spermatheca; 33. *Merope tuber* Newm. ♀, reproductive organs; 33a, *Merope tuber* Newm. ♀, spermatheca.

a, anus; ac, accessory gland; acd, accessory gland duct; acl, lateral accessory glands; aco, accessory duct opening; as, abdominal segment; ca, capsule; co, common oviduct; e, epididymis; ej, ejaculatory duct; ejs, ejaculatory sac; fe, follicle; is, intersegmental membrane; go, gonopod; gp, gonopore; h, hind gut; o, ovariole; ov, oviduct; r, rectum; sp, spermatheca; spd, spermathecal duct; spo, spermathecal duct opening; t, testis; v, vesicula seminalis; vd, vas deferens; ve, vas efferens.

Bittacus pilicornis Westw. (fig. 25). A short and not completely accurate description of the male organs of *Bittacus italicus* Mull. is given by Stitz (1926). Brauer (1855) stated that there are three follicles in *Bittacus tipularius* Latr. (*italicus*), but figured four.

The testes are enclosed in a common sac and lie in the mid line in segments 7 and 8 over the S bend of the hind gut and the base of the mid gut. The vasa deferentia emerge from either side of the base of the common sac. Each vas deferens runs for a short distance posteriorly, before turning and running anteriorly with the other in the mid line. They adhere closely and apparently fuse, but separate in the 7th segment just before each enters the apex of the vesicula seminalis (v) of its side. Each vesicula seminalis bears laterally a relatively long accessory gland (ac), slightly exceeding itself in length. The vesiculae seminales at their posterior ends make a short bend away from each other, but enter the swollen ductus ejaculatorius (ej) together.

The ductus appears to open in the aedeagus, under a small cuticularised tongue, into a hollow, which extends into a long coiled flagellum (fl). The latter is coiled like a watch spring and when extended is longer than the entire length of the insect.

The testes lie directly above the vesiculae seminales, because the vasa deferentia are short. The testes are closely applied to each other within the common sac and each consists of four pink follicles (fe). At its posterior end each follicle has a small white cap from which a very short vas efferens goes to unite with those of the other three follicles. The vas deferens coils into a compact epididymis (e), which adheres to the posterior end of the testis and which can be seen as a protuberance in the common sac. The vas deferens on leaving the epididymis passes out of the common sac at its base.

Harpobittacus tillyardi Ebsen-Peters. (fig. 26). The testes lie pressed together in the mid line above the gut, but there is no common sac. Each testis consists of four follicles (fe). Three-quarters of the length of the follicle is dark purple; the remainder is white. The follicles of each testis open into the vas deferens which bends ventrally under the testis and then runs posteriorly forming a coiled epididymis (e). The tube becomes finer and emerges to run posteriorly towards the mid line. In the 8th segment the two vasa deferentia adhere and the apparently single tube runs forward to the proximal margin of the 6th segment, where it divides and each branch enters one of the pair of vesiculae seminales (v), which extend posteriorly into the 8th segment. In the 7th segment a large accessory gland (ac) arises from the outer side of each vesicle and lies parallel with it, but slightly exceeding it in length. The vesiculae seminales are abruptly constricted at the distal margin of the 8th segment and the narrow ducts pass side by side ventrally and then posteriorly to enter the swollen ejaculatory duct, which is deeply grooved dorsally and produced into a membranous flap.

Apterobittacus apterus McL. The two testes lie in a common sac on the dorsal surface of the gut immediately anterior to the S bend of the hind gut and in the posterior part of segment 6. The two testes are closely adpressed within the sac. Each consists of four follicles, the vasa efferentia of which are very short. Each vas deferens is coiled and then forms an epididymis which also lies within the testicular sac, pressed against the posterior end of the testis. The vasa deferentia leave the sac and pass on either side of the body to the posterior part of the 8th segment, where they meet in the mid line. They are thicker than when forming the epididymis. They adhere and run forwards into the anterior part of the 7th segment, where they separate and each enters the apex

of its respective vesicula seminalis. The vesiculae seminales extend posteriorly into the posterior part of the 8th segment, where they receive the pair of lateral accessory glands which lie parallel with them, but which are slightly longer and thicker. The vasa deferentia continue posteriorly, bend ventrally and unite just before entering the swollen ejaculatory sac. A pair of short bent accessory glands arise from the dorsal wall of the ejaculatory sac at its anterior end.

The general structure of the male organs of *Bittacus*, *Harpobittacus* and *Apterobittacus* is similar, but they differ in the relative proportions of the parts. *Apterobittacus* seems to be intermediate between *Bittacus* and *Harpobittacus*. Its testes are smaller than those of *Bittacus* but larger than those of *Harpobittacus*. Its vesiculae seminales are larger than those of *Bittacus*, but not so large as those of *Harpobittacus*. It has glands, associated with the ejaculatory sac, which are not found in the other two genera. The testes and epididymis are contained in a common sac as in *Bittacus*.

Female reproductive organs.

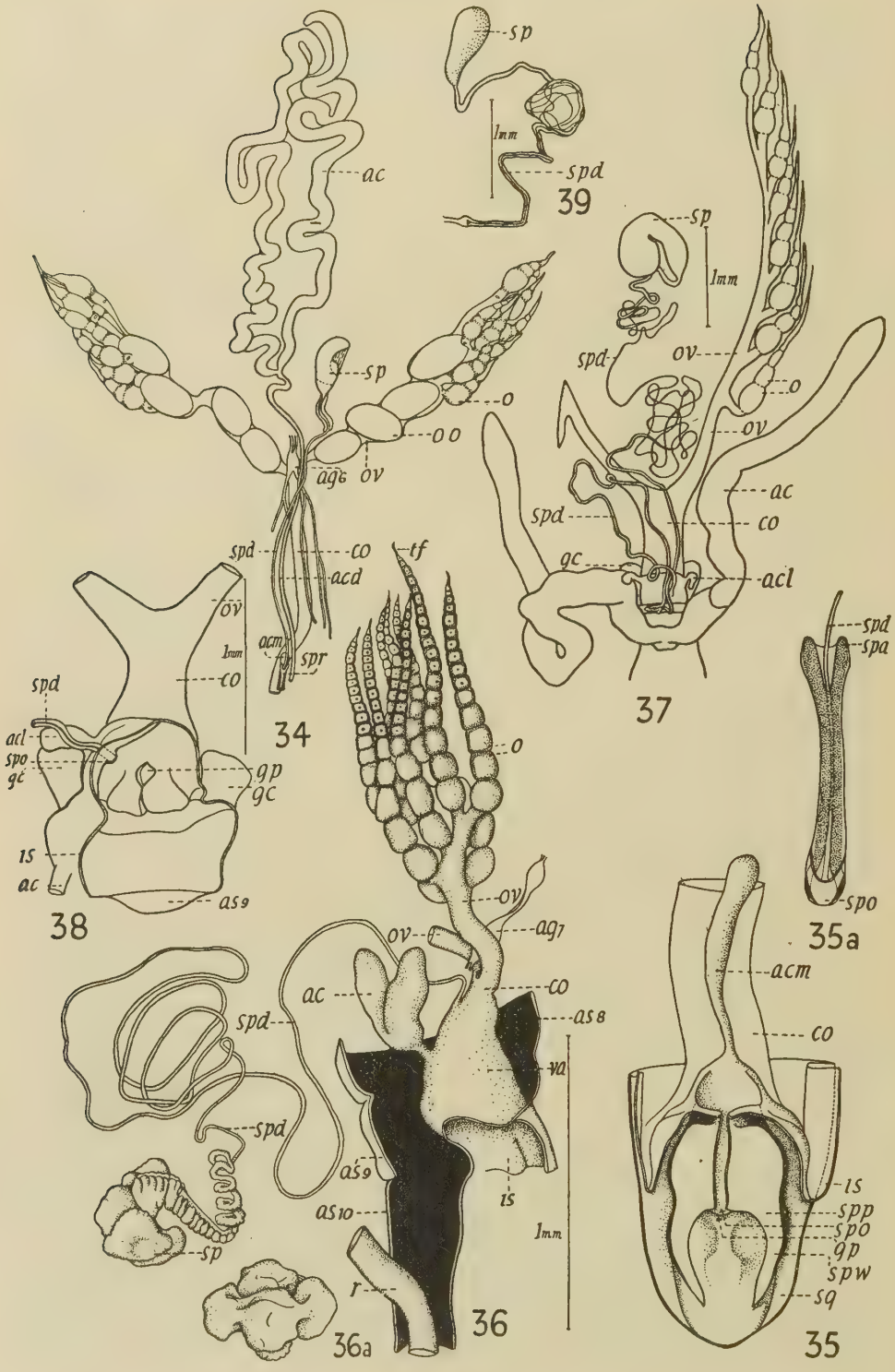
Brachypanorpa carolinensis Banks. The female material of this genus was not preserved until it had been dead a few hours. This probably accounts for the fact that the organs had adhered to the body wall and were not dissectable.

Chorista australis Klug (figs. 31, 32). The ovaries are similar in structure to those of *Panorpa*, but each ovary consists of seven ovarioles. The oviducts unite in the 7th segment. The common oviduct is a stout tube slightly folded to allow extension of the abdomen and opens into the anterior end of the genital pouch.

The spermatheca (sp) is an oval, white, opaque body, similar in size to a mature oocyte and lies on the junction of the oviducts. The spermathecae duct (spd) is a relatively thick tube and is much coiled. It lies upon the common oviduct and opens upon a papilla (spo) on the dorsal wall of the genital pouch, posterior to the genital opening (gp).

The accessory glands (ac) consist of a pair of thick, white and much coiled tubes lying in the abdomen ventral to the ovaries. The glands unite in the 8th segment to form a common duct, which opens posteriorly to the spermathecal duct on the dorsal wall of the genital pouch.

Boreus hyemalis L. (figs. 36, 36a). A brief description of the female reproductive organs of *B. hyemalis* is given by Brauer (1855) and Steiner (1937). My conclusions are not in entire agreement with these authors. Each ovary consists of eight ovarioles opening separately into the oviduct; Brauer (1855) stated that there are ten ovarioles in this species. The end filaments of the ovarioles unite to form a common thread, which joins that of the other ovary. The oviducts (ov) of either side unite in the 6th abdominal segment to form the short common oviduct (co). The seventh abdominal ganglion (ag 7) lies between the oviducts in the fork of their junction. The common oviduct enlarges into the vagina (va). There is no external distinction between the two regions apart from size, but according to Snodgrass' (1933) definition the genital chamber lies posterior to the opening of the spermathecal duct, the common oviduct anterior. When the chamber takes the form of a tubular passage it is called the vagina. The vagina is wide and pouch-like and receives the openings of the spermathecal duct and accessory gland on its dorsal surface. Its dorsal wall is continuous with the intersegmental membrane and its ventral wall with the 9th sternite.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The vagina is supported laterally by strong muscles and two muscles are attached to it dorsally just anterior to the opening of the spermathecal duct. Fig. 36 shows the spermatheca (sp) and its duct (spd) uncoiled and spread out. In its natural position the spermathecal duct is coiled like a watch spring and pressed flat against the dorsal surface of the vagina. The glandular part of the duct is also tightly coiled and closely applied to the spermatheca, which is folded and squeezed between the accessory gland and its own coiled duct. The spermatheca (sp) consists of a median lobe, two lateral lobes opening out of the median lobe and a large median, ventral, membranous sac. The duct is large and thick-walled close to the spermatheca, but the tube narrows and the walls lose their glandular appearance after a few tight coils. The remainder of the duct is very fine and of considerable length. The accessory gland (ac) consists of two large pouch-like glands which open into a short common duct. It lies in an upright position beside the vagina, pressed against the spermatheca and its coiled duct. The opening of the accessory gland into the vagina is posterior to that of the spermatheca. Steiner (1937) suggests that the so-called accessory gland may be a bursa copulatrix. This seems unlikely when the organ is compared with the accessory glands of other genera.

Merope tuber Newm. (figs. 33, 33a). The ovaries lie in the 5th and 6th abdominal segments. In the specimen figured there were 9 ovarioles in the left ovary and 8 in the right. The ovarioles (o) open laterally into the oviduct and the two oviducts unite in the posterior part of the 6th segment; the 7th and last abdominal ganglion lies on the fork formed by their union. The common oviduct (co) is a wide tube passing through segments 6, 7 and 8 to open into the anterior end of the genital pouch. The spermatheca (sp) lies above the junction of the oviducts. It is a large pear-shaped cuticularised body. The duct is wide at its origin, but narrows as it passes posteriorly, closely adhering to the spermatheca. At the posterior end of the spermatheca it becomes exceedingly fine. This fine tube coils repeatedly, forming a coat over the spermatheca. Finally the duct leaves the coils and rises over the junction of the oviducts, growing larger in diameter, and runs posteriorly along the dorsal surface of the common oviduct. It opens into the genital pouch just dorsal to the opening of the common oviduct. The two coiled accessory glands (ac) unite behind the junction of the oviducts, and the common accessory gland so formed runs posteriorly above the common oviduct and the spermathecal duct. It opens into the genital pouch through two fleshy lips, posterior to the opening of the spermathecal duct. On either side of the posterior third of the common accessory duct lies a sac-like accessory gland (acl) with a reticulate pattern on its surface. These two sac-like glands were

FIGS. 34–39.—Female reproductive organs. 34. *Panorpa germanica* L.; 35. *Panorpa germanica* L., genital pouch opened to show spermathecal pocket and opening of common oviduct. The spermathecal rod has been removed; 35a. *Panorpa germanica* L., spermathecal rod dissected out of its pocket; 36. *Boreus hyemalis* L.; 36a. *Boreus hyemalis* L., dorsal view of spermatheca; 37. *Bittacus pilicornis* Westw.; 38. *Bittacus pilicornis* Westw., genital pouch opened to show openings of common oviduct, spermathecal duct and accessory gland; 39. *Harpobittacus tillyardi* E.-P., spermatheca and duct.

ac, accessory glands; acd, duct of accessory gland; acm, median accessory gland; acl, lateral accessory glands; ag, abdominal ganglia; as, abdominal segment; co, common oviduct; gc, genital pouch; gp, gonopore; o, ovariole; oo, oocyte; ov, oviduct; sp, spermatheca; spa, arms of spermathecal rod; spd, duct of spermatheca; spo, opening of spermathecal duct; spp, spermathecal pocket; spw, wings of spermathecal pocket; spr, spermathecal rod; r, rectum; va, vagina.

empty in this specimen and folded inwards on their ventral surface. They open into the vaginal pouch on either side of the common accessary duct opening.

Bittacus pilicornis Westw. (figs. 37, 38). Stitz (1926) gave a short inaccurate description of the female organs. Brauer (1855) gave a brief description of *Bittacus tipularius* Latr. (*italicus*) and said that there are 10 ovarioles in each ovary.

In *B. pilicornis* each ovary consists of 8 ovarioles opening laterally into the oviduct. The two ovaries overlie the gut and the apices of the ovarioles meet in the mid line of the body. The oviducts (ov), below the entrance of the most posterior ovariole, run towards the mid line of the abdomen and unite in the posterior part of the 7th segment. The common oviduct (co) is wide and muscular and opens into an invagination or infolding of the genital pouch. The walls of this invagination are very thick and muscular. It is slit dorsally so that two lateral fleshy lips are formed. This slit widens slightly at its anterior end forming an opening into the common oviduct, and it is just above this opening that the spermathecal duct (spo) opens on the dorsal wall of the genital pouch. The spermathecal duct is produced into a cornicle, which fits into the opening of the common oviduct.

On either side of and ventral to the invagination of the common oviduct, the genital pouch is expanded into a lateral pouch. Two small accessory glands (acl) open into the pouch, lateral to and above the invagination of the oviduct. The spermatheca (sp) lies above the junction of the oviducts, partly in the 7th and partly in the 8th segment. It is a short thick tube with a globular apex, bent upon itself. The duct is very fine and forms a closely interlaced coat over the surface of the spermatheca. The tube thickens and leaves the coat to run posteriorly on to the dorsal surface of the genital pouch. Here it passes over and under a muscle which is stretched across the body cavity above the pouch. It adheres to the underside of the muscle and then turns to pass again over the muscle, coil over the common oviduct and in the 7th segment turns posteriorly again and opens on the dorsal wall of the genital pouch as described above.

The two thick and relatively long accessory glands (ac) enter the short common duct (acd), which opens into the posterior part of the dorsal wall of the genital pouch.

The genital pouch is large and its walls are deeply infolded.

Harpobittacus tillyardi Esben-Peters. (fig. 39). The system is very similar to that of *Bittacus pilicornis* Westw. The spermatheca (sp) is pear-shaped and straight, not bent on itself as in *Bittacus*. The spermathecal duct on leaving the spermatheca is at first thick, but gradually becomes very fine and forms a close mat over the spermatheca. The duct leaving this mat is thick-walled and the lumen is seen as a brown line in the centre of the tube. The free part of the duct is comparatively short. Just before entering the genital pouch it is slightly swollen, and the brown line terminates in a cup-shaped expansion. The short duct may be correlated with the short flagellum of the male. The duct opens into the genital pouch above the invaginated common oviduct, as in *Bittacus*.

The two accessory glands extend into the 4th abdominal segment and lie parallel with the gut. They run towards each other in the 8th segment and passing posteriorly, unite in a short common duct.

Apterobittacus apterus McL. (fig. 51). The ovaries are similar in structure to those of *Bittacus* and *Harpobittacus*, but the ovarioles are more numerous.

In one specimen there were 14 ovarioles in each ovary, in another there were 16 in one ovary and 19 in the other.

The oviducts unite in the mid line in the posterior part of the 7th segment where their junction is covered by the last nerve ganglion. The accessory glands (ac) are very long and extend into the 2nd abdominal segment. They unite towards the posterior margin of the 8th segment and pass by a short common duct into the genital pouch. A small median pouch-like gland (acm) arises from the common duct just before it enters the genital pouch.

The spermatheca (sp) is pear-shaped and straight, but the first part of its duct is thick and lies against it. The duct (spd) narrows abruptly into a thread-like tube which forms a dense coiled knot just posterior to the spermatheca. A short duct leaves the knot and enters (spo) the genital pouch behind a sac-like dorsal expansion.

This spermatheca is intermediate between those of *Bittacus* and *Harpobittacus*.

Terminal segments of the female abdomen.

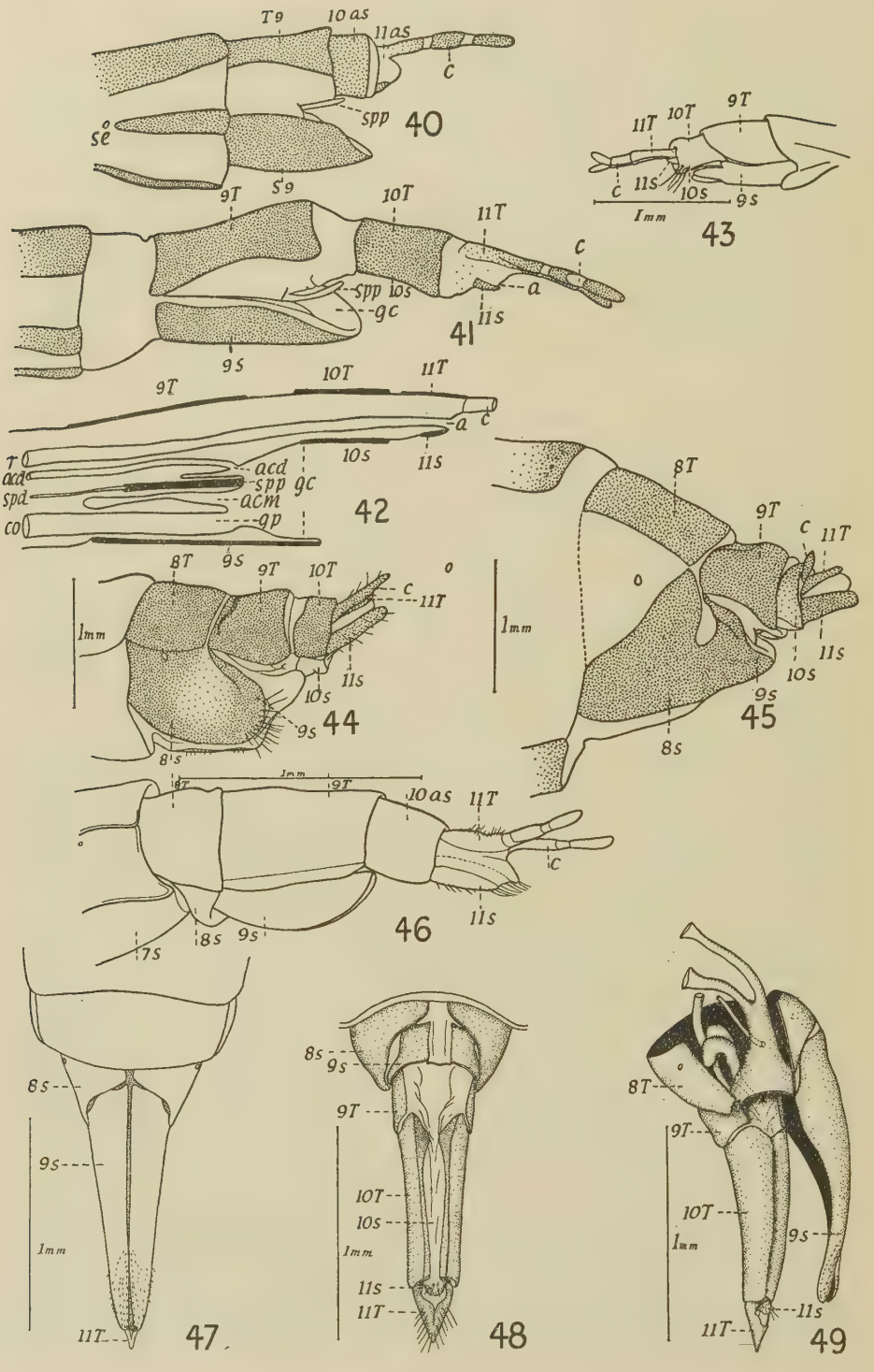
Brachypanorpa carolinensis Banks (fig. 52). The 6th segment is normal. The 7th is annular and is partially retracted into the 6th. The 8th is also annular and is retracted within the 7th. The intersegmental membrane between segments 6 and 7, and 7 and 8 is strengthened by longitudinal cuticular struts; two dorsal, two ventral and one on each side. The tergite of the 9th segment has a median sclerotised band and two lateral bands separated by membrane. The sternite is scoop-shaped and its free lip is pressed against segment 10, closing the genital opening. The 9th sternite is capable of considerable expansion by reason of a median membranous band. The 10th segment is annular. The 11th sternite is a small flap-like lobe and the two segmented cerci (c) arise from the apex of the 11th tergite.

Chorista australis Klug (fig. 43). The 8th segment is normal. The 9th sternite is produced to form the subgenital plate and consists of two cuticularised plates separated by membrane. This median membrane is invaginated so that the genital pouch, of which it forms the floor, can expand. The free apex of the sternite is deeply cleft, and the two lobes, so formed, carry two smaller lobes on their outer margins. The 9th sternite is free from its tergite for about two-thirds of its length. The 10th and 11th segments are similar to those of *Panorpa*, the 11th carries a pair of two-segmented cerci.

Boreus hyemalis L. (figs. 47, 48, 49). There is considerable confusion in the literature as to the homologies of the terminal segments of the abdomen. Most authors merely state that the end of the abdomen is drawn out into an ovipositor protected by a bilobed process. Westwood (1840) on *B. hyemalis*, Dohanian (1915) on *B. brumalis* Fitch, and Carpenter (1931) on American species, think that the " process " arises from the 7th segment. Stitz (1908) partially described the abdomen of *B. hyemalis*, but did not homologise the parts, nor did Withycombe (1921).

Although the abdomen has the appearance of an ovipositor it is not morphologically one.

The 7th segment is normal. The 8th segment is an almost complete ring, there being a narrow membranous area in the mid ventral line. Its posterior ventral margin is deeply concave and in this concavity is inserted the base of the bilobed 9th sternite. This 9th sternite (9S) consists of two sclerites which are connected by membrane for two-thirds of their length, but which are free for the terminal third. The 9th tergite (9T) forms an incomplete ring, the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ventral part of the ring being membranous. This membrane is continuous with the membrane of the genital chamber and continuous with the membranous lining of the 9th sternite. It is also continuous posteriorly with the 10th segment. The opening of the vagina lies dorsal to the base of the 9th sternite and there is no true ovipositor. The relationship of the reproductive organs to the terminal abdominal segments is shown in fig. 49. The common oviduct (co) opens into the cavity formed by the invagination of the membrane between the 9th sternite (9S) and the 10th segment (10 leave). Snodgrass (1933) defined the subgenital plate as the sternite which conceals the genital cavity. The term subgenital plate may therefore refer to the 7th, 8th or 9th sternite according to the species of insect in question. In the genus *Boreus*, as in *Panorpa*, the 9th sternite is the subgenital plate; the 9th sternite in *P. communis* L. is a single plate; in *P. nipponensis* Nav. the 9th sternite is composed of two sclerites joined by membrane (Miyake 1913), but in *Boreus hyemalis* the separation of the sternite into two parts has gone farther and the sclerites are free at the distal apex.

The genital chamber of *B. hyemalis* is so deeply invaginated into the body as to conform to Snodgrass' (1933) definition of a vagina.

The 10th tergite is long. The tergite is strongly sclerotised and its lateral margins are infolded on the ventral surface. The sternite is membranous and very much folded longitudinally. The 11th tergite is heavily cuticularised and is shaped like the toe of a shoe, its apex sharply pointed. A small hairy pad, the 11th sternite, lies on the membrane at the base of the 11th segment, between the inrolled margins of the tergite. The anus lies below the 11th sternite. There are no cerci.

The hollowed, membranous sternite of the 10th segment together with the concave 9th sternite form an incomplete tube, by means of which the egg can be guided to a suitable position. The so-called ovipositor, although not morphologically one, functions as such.

Merope tuber Newm. (fig. 46). The 8th segment is deeply retracted into the 7th and its spiracle is not visible. The 9th sternite is produced very little beyond the 9th tergite and is strongly convex. This convexity causes the apex of the sternite to press against the intersegmental membrane between segments 9 and 10 and so to close the genital pouch. The sternite is infolded in the mid line. It is cleft apically and is only separated for a short distance from the 9th tergite.

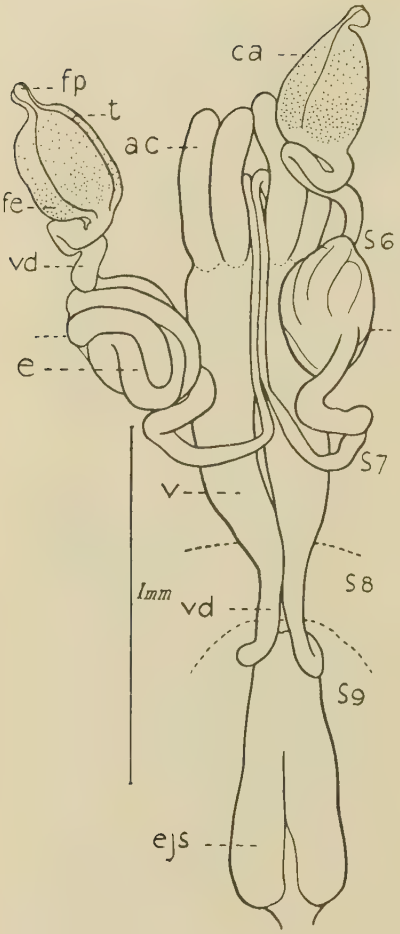
The 10th segment is completely cuticularised. The 11th segment consists of a tergal plate, from which arise the two-segmented cerci, and a sternal plate.

Bittacus pilicornis Westw. (fig. 44). The 7th segment is normal.

The 8th sternite consists of two lateral cuticularised plates separated by membrane in the mid-ventral region. It is produced forwards so as to lie below the 9th tergite. The 9th tergite is normal with a dark band near the proximal dorsal margin and it is slightly telescoped within the 8th segment.

Figs. 40–49.—End of female abdomen. 40. *Panorpa communis* L. ♀; 41. *Panorpa communis* L. ♀, extended; 42. *Panorpa communis* L. ♀, diagrammatic; 43. *Chorista australis* Klug ♀; 44. *Bittacus pilicornis* Westw. ♀; 45. *Harpobittacus tillyardi* E.-P. ♀; 46. *Merope tuber* Newm. ♀; 47. *Boreus hyemalis* L. ♀, ventral view; 48. *Boreus hyemalis* L. ♀, ventral view, 9th sternite removed; 49. *Boreus hyemalis* L. ♀, showing reproductive organs in relation to the terminal segments.

a, anus; acd, duct of accessory glands; acm, median accessory gland; c, cercus; gc, genital pouch; gp, genital pore; r, rectum; s, sternite; se, spiracle; spd, spermathecal duct; spp, spermathecal pocket; T, tergite.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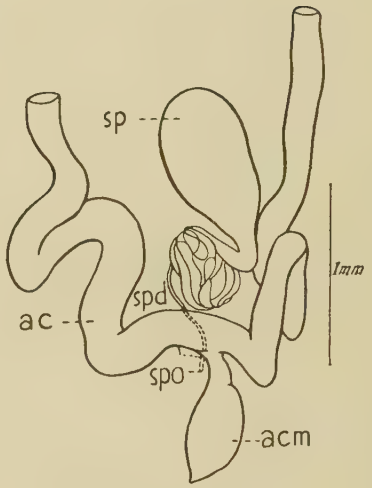
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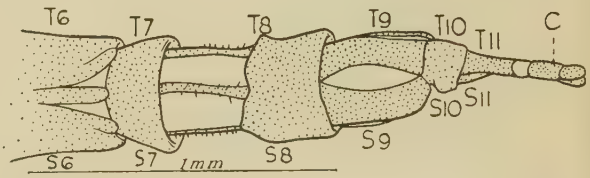
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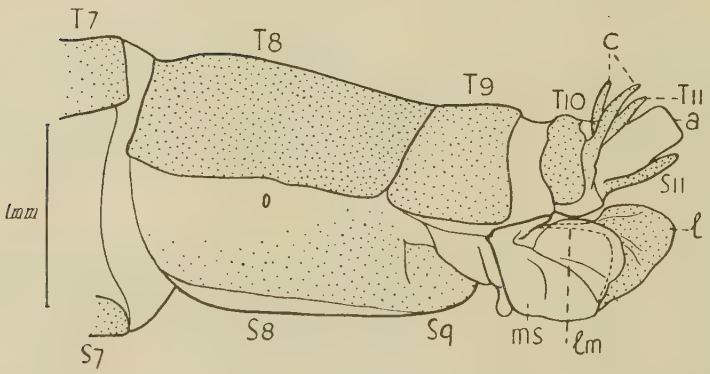
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The 9th sternite appears to consist of a median membranous lobe produced very slightly and bent dorsally so as to protect the opening of the genital pouch. It passes insensibly into the median membranous region of the 8th sternite. Laterally a narrow, cuticularised arm which is fused with the 8th sternite unites at its apex with the proximal lateral margin of the 9th tergite and appears to belong to the 9th segment. This attachment is usually telescoped within the 8th segment. The 9th sternite would therefore appear to be completely fused with the 8th.

The tergite of the 10th segment is cuticularised; the sternal region is membranous and infolded. The 11th segment consists of a tergal and sternal plate and carries the anus at its apex. The unsegmented cerci arise laterally between the 10th and 11th segments.

Harpobittacus tillyardi Ebsen-Peters. (fig. 45). The 7th segment is normal.

The 8th sternite is widely separated from the tergite by the broad pleural membrane at the proximal border of the segment, but on the distal border the tergite and sternite touch. The 8th spiracle lies in the membrane. The sternite is divided longitudinally on the mid-ventral surface by a band of membrane wider on the proximal margin of the segment than on the distal. The fusion of the 8th and 9th sternites is not so complete as in *Bittacus pilicornis* Westw. A deep membranous indentation, continuous with the intersegmental membrane, separates the two sternites laterally. Ventrally the fusion is complete. This compound subgenital plate projects slightly to protect the genital opening.

The 9th tergite is concave on the dorsal proximal area and is swollen into a dorsal ridge on the distal margin. The tergite covers the sides of the segment.

The dorsal part of the 10th segment is cuticularised, the sternal region is membranous. The unsegmented cerci arise from its distal border. The tergite and sternite of the 11th segment are fully developed and elongate. The anus opens at the apex of the segment.

Apterobittacus apterus McL. (fig. 53). The tergite of the 8th segment is normal; the sternite consists of two bands of cuticle which touch distally but which become narrower and separate proximally. The pleural membrane is wide and passes imperceptibly into the sternite. The 9th tergite is normal. The junction of the 8th and 9th sternites is indicated by a lateral fold which disappears ventrally. The distal part of the 9th sternite is expanded into a membranous sac (ms), which lies below the 10th segment, and which passes into a brown lobe (l) lying below the 11th segment. To the proximal dorsal margin of the lobe is attached a longitudinal muscle (lm) which can be seen through the walls of the membranous 9th sternite.

Between the membranous lobe and the cuticularised part of the 9th sternite projects a small median lobe.

The 10th tergite is cuticularised; the sternite is membranous. The 11th segment consists of dorsal and ventral plates, between which protrudes the

FIGS. 50–53.—50. *Brachypanorpa carolinensis* Banks, male reproductive organs; 51, *Apterobittacus apterus* McL., female, spermatheca and accessory glands; 52. *Brachypanorpa carolinensis* Banks, end of female abdomen; 53. *Apterobittacus apterus* McL., end of female abdomen.

a, anus; ac, accessory gland; acm, median accessory gland; c, cercus; ca, capsule; e, epididymis; ejs, ejaculatory sac; fe, follicle; fp, follicular process; l, brown lobe; lm, lobular muscle; ms, membranous sac; s, sternite; sp, spermatheca; spd, spermathecal duct; spo, spermathecal duct opening; t, testis; T, tergite; v, vesicula seminalis; vd, vas deferens.

anal tube (a). The anal cerci (c) arise from the membrane between segments 10 and 11.

The dorsal vessel.

The dorsal vessel was only dissected in *Boreus hyemalis* L., the remaining material being not sufficiently fresh.

Boreus hyemalis L. The dorsal vessel is a straight tube. The aorta in the thorax is extremely fine, but the heart gradually widens towards the posterior end of the abdomen. The heart is lined by an irregular layer of cells—the dorsal nephrocytes.

Comparison of the Internal Organs of the Mecoptera.

Alimentary canal. The digestive system is generally similar in the eight genera, but the proportionate length of the three divisions of the canal vary in the different genera. *Panorpa*, *Brachypanorpa*, and *Chorista* are very similar and have a short fore gut, medium mid gut and long hind gut. The fore and hind guts of *Bittacus* are short and the mid gut is very long. *Boreus* and *Merope* have fore and mid guts of equal length, but the hind gut is almost as long as the fore and mid guts together.

There are six malpighian tubules in all the families.

The proventriculus is similar in structure throughout the order.

Six rectal glands are present in all the families except the Boreidae.

The salivary glands. These glands are present, but differ considerably in structure in each family. Sexual dimorphism occurs only in *Panorpa.*

Nervous system. Sexual dimorphism in the number of free abdominal ganglia is shown by all the genera with the exception of *Boreus.* The male has, in each species, one more free abdominal ganglion than the female. *Merope* male has eight free abdominal ganglia, *Panorpa*, *Brachypanorpa*, *Chorista*, and *Boreus* males have seven and *Bittacus*, *Harpobittacus*, and *Apterobittacus* males have six. In the latter genera the first true abdominal ganglion is fused with the metathoracic ganglion.

The brain is similar in shape in the different genera, although it is deeper and narrower in *Boreus* and *Merope.*

There are three dorsal ocelli in all except *Merope.*

The recurrent nerve of the sympathetic system is two-branched in *Panorpa*, *Brachypanorpa*, *Chorista*, *Merope* and *Apterobittacus*, but single in *Boreus.*

Male reproductive system. There is considerable general resemblance between the male organs of *Panorpa*, *Brachypanorpa*, *Chorista*, *Bittacus*, *Apterobittacus*, and *Harpobittacus*, the main differences being ones of proportion. The sizes of the epididymis, accessory glands and testes varies in relation to the size of the whole system.

Accessory glands are small in *Panorpa communis* L., medium in *Brachypanorpa*, wanting in *Chorista*, present in *Bittacus*, medium in *Apterobittacus*, and very large in *Harpobittacus.* According to Miyake (1913) there is considerable difference in the length of the accessory glands in different species of *Panorpa*, so that size may be a variable character in this organ.

The general shape of the testis is similar in all the genera except *Boreus.* There are three follicles in each testis in *Panorpa*, *Brachypanorpa*, and *Chorista* and four in *Merope*, *Bittacus*, *Apterobittacus*, and *Harpobittacus.* The two testes lie in a common sac in *Merope*, *Bittacus*, and *Apterobittacus*, but are separate in the other families with the exception of *Boreus.*

An epididymis is present in all but *Boreus*, although that of *Merope* is small.

The length of the ductus ejaculatorius seems to depend on the position of the organs in the body. It is very short in *Brachypanorpa*, *Chorista*, *Bittacus*, *Apterobittacus*, and *Harpobittacus*, long in *Merope* and *Boreus*, and very long in *Panorpa*.

The testes, accessory glands and vesiculae seminales lie in the median ventral line of the abdomen, but *Merope* is unique, in that, although the testes are median in position, the ducts and vesiculae seminales lie in the base of the right gonocoxite.

The reproductive system of *Boreus* bears very little resemblance to that of the other families.

Female reproductive system. The ovaries are similar throughout the order; they differ chiefly in the number of the ovarioles.

Accessory glands are universally present. They vary in size from relatively very large in *Panorpa*, *Chorista*, and *Apterobittacus*, medium in *Merope* and *Bittacus*, to short and compact in *Boreus*.

There is one spermatheca which differs in shape in the six families, and is especially modified in *Boreus*.

The outstanding feature of the system is the remarkable length of the spermathecal duct, especially in *Boreus*, *Merope*, *Bittacus*, *Apterobittacus*, and *Harpobittacus*. The reason for this is difficult to see, for except in the case of *Bittacus pilicornis* Westw., it is not correlated with the length of the aedeagus in the male.

The oviducts, spermathecal duct and accessory glands open into the genital pouch, except in *Boreus*, where a vagina has been formed by the invagination of the pouch.

Additional accessory glands are found in *Panorpa*, which has a single median gland, in *Merope*, which has two lateral glands, and in *Bittacus* which also has two lateral glands.

Only in *Panorpa* does the spermathecal duct open on a sclerotised structure.

Female abdomen. The genital opening lies between segments 9 and 10 on the intersegmental membrane, which is invaginated to form the genital chamber.

The 9th sternite or subgenital plate is greatly modified in *Boreus*, but only slightly so in the other families.

The 8th and 9th sternites of *Bittacus* and *Harpobittacus* are fused, the fusion being most complete in *Bittacus*. The genital opening appears, therefore, to lie between segments 8 and 9.

There are 11 segments in all the families, and cerci are present in all except *Boreus*. The cerci are borne on the 11th segment in *Panorpa*, *Brachypanorpa*, *Chorista*, and *Merope* and between 10 and 11 in *Bittacus*, *Harpobittacus*, and *Apterobittacus*.

Conclusions.

It is clear from the above comparisons that the characters of the family Boreidae have diverged very widely from the general Mecopterous structure. The external morphological characters, such as the mouthparts and the terminal abdominal segments, are less specialised than the internal ones. It has retained the Mecopterous type of proventriculus, but has lost the typical rectal glands, and the dimorphism of the abdominal ganglia. The reproductive system is also much modified.

It seems that *Boreus* must have specialised very early in the history of the order.

The most striking of the typically Mecopterous characters of the order are the proventriculus, the rectal glands, the dimorphic abdominal ganglia (which character is also found in the Aphaniptera), the long spermathecal duct and the eleven segmented abdomen.

References.

Brants, A., 1839, Ontleedkundige Beschouwing van de Schorpioenvlieg *Panorpa communis*. *Tijds. nat. Geschied* **6** : 173–198.

Brauer, F., 1855, Beitrage zur Kenntnis des inneren Baues und der Verwandlung der Neuropteren. *Verh. zool. bot. Ges. Wien* **5** : 701–726.

Carpenter, F. M., 1931, Revision of the Nearctic Mecoptera. *Bull. Mus. comp. Zool.* **72** : 205–277, 8 pls.

Dufour, L., 1841, Récherches anatomique et physiologique sur les Orthoptères, les Hyménoptères et les Neuroptères. *Mem. Sav. étrang. Acad. Sci. Paris* **7** : 265–647, 212 figs.

Esben-Petersen, P., 1921, Mecoptera. *Coll. zool. Selys Longchamps* **5** (2), 2 pls., 188 figs.

Gross, J., 1903, Untersuchungen über die Histologie des Insektenovariums. *Zool. Jahrb.* (Anat.) **18** : 100–103, 8 pls., 8 figs.

Issiki, S., 1933, Morphological studies on the Panorpidae of Japan and adjoining countries and comparison with American and European forms. *Jap. J. Zool.* **4** : 315–416, 45 figs.

Loew, H., 1848, Abbildungen und Bemerkungen zur Anatomie einiger Neuropteren-Gattungen. *Linn. Ent.* **3** : 363–375.

Mercier, L., 1916, Caractère sexuel secondaire chez les Panorpes. Le rôle des glandes salivaires des males. *Arch. Zool. exp. gén.* **55** (Notes et Revue) : 1–5.

——, 1920a, Les glandes salivaires des Panorpes sont elles sous la dépendence des glandes génitales? *C.R. Soc. Biol. Paris* **72** : 470–471.

——, 1920b, Les papilles rectales des Panorpes. *C.R. Soc. Biol. Paris* **72** : 758–760.

Miyake, T., 1912, The life history of *Panorpa klugi* M'Lachlan. *J. Coll. Agric. Tokyo* **4** : 117–139, 2 pls.

——, 1913, Studies on the Mecoptera of Japan. *J. Coll. Agric. Tokyo* **4** : 265–400.

Snodgrass, R. E., 1931, Morphology of the insect abdomen. Part 1. General structure of the abdomen and its appendages. *Smithson. misc. Coll.* **85** : 128 pp., 46 figs.

——, 1933, Morphology of the insect abdomen. Part 2, The genital ducts and the ovipositor. *Smithson. misc. Coll.* **89** : 148 pp., 48 figs.

——, 1935, *Principles of insect morphology.*

Steiner, P., 1937, Beitrage zur Fortpflanzungsbiologie und Morphologie des genitalapparates von *Boreus hiemalis* L. *Z. Morph. Oekol. Tiere.* **32** : 276–288, 6 figs.

Stitz, H., 1908, Zur Kenntnis des Genitalapparats der Panorpaten. *Zool. Jahrb.* (Anat.) **26** : 537–564, 2 pls.

——, 1926, Mecoptera. *Biol. Tiere Deutschl.* **21** (35) : 28 pp., 44 figs.

Wigglesworth, V. B., 1932, Function of the rectal glands. *Quart. J. micr. Sci.* **75** : 131–150.

Withycombe, C. L., 1921, On the life history of *Boreus hyemalis* L. *Trans. ent. Soc. Lond.* **1921** : 312–318, 1 pl., 3 figs.

List of Abbreviations.

a, anus.
ac, accessory gland.
acd, accessory gland duct.
acl, lateral accessory gland.
acm, median accessory gland.
aco, accessory duct opening.
ag, abdominal ganglia.
al, antennary lobe.
ao, aorta.
as, abdominal segment.
b, brain.
c, cercus.
ca, testicular capsule.
co, common oviduct.
cp, corpus allatum.
e, epididymus.
ej, ejaculatory duct.
ejs, ejaculatory sac.
f, frontal ganglion.
fc, frontal ganglion connectives.
fe, follicle.
fl, flagellum.
fp, follicular process.
g, salivary gland.
gc, genital pouch.
go, gonopod.
gp, gonopore.
h, hind gut.
hy, hypopharynx.
is, intersegmental membrane.
l, brown lobe.
lm, lobular muscle.
m, mid gut.
mp, malpighian tubule.
ms, membranous sac.
o, ovariole.
oc, ocellus.
oe, oesophagus.
og, occipital ganglion.
oo, oocyte.
ov, oviduct.
p, proventriculus.
ph, pharynx.
pht, pharyngeal trough.
pl, lateral arms of pharyngeal trough.
r, rectum.
rg, rectal glands.
rn, recurrent nerve.
rn_1, rn_2, branches of recurrent nerve.
s, sternite.
sc, common salivary duct.
sd, salivary duct.
se, spiracle.
sp, spermatheca.
spa, arms of spermathecal rod.
spd, duct of spermatheca.
spo, opening of spermathecal duct.
spp, spermathecal pocket.
spw, wings of spermathecal pocket.
spr, spermathecal rod.
spn, spiracular nerve.
sr, salivary reservoir.
T, tergite.
t, testis.
tg, thoracic ganglion.
v, vesicula seminalis.
va, vagina.
vd, vas deferens.
ve, vas efferens.